

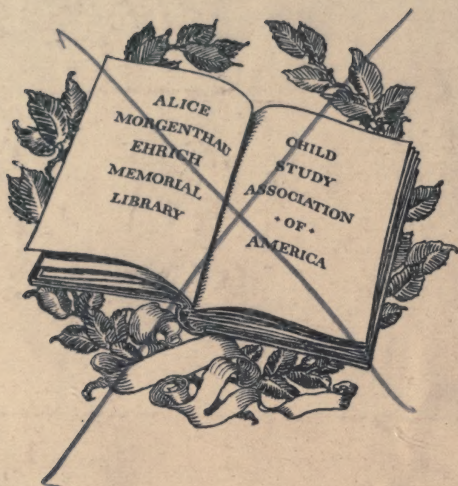
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BEING WELL-BORN

Michael F. Guyer



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BEING WELL-BORN

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Being Well-Born

AN INTRODUCTION TO HEREDITY
AND EUGENICS

By

Frederic

MICHAEL F. GUYER

Professor of Zoology, The University of Wisconsin

[2d ed.]

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TO MY WIFE

HELEN M. GUYER

Faithful critic, inspiring friend

PREFACE TO THE FIRST EDITION

One of the most significant processes at work in society to-day is the awakening of the civilized world to the rights of the child; and it is coming to be realized that its right of rights is that of being well-born. Any series of publications, therefore, dealing primarily with the problems of child nature may very fittingly be initiated by a discussion of the factor of well-nigh supreme importance in determining this nature, heredity.

No principles have more direct bearing on the welfare of man than do those of heredity, and yet on scarcely any subject does as wide-spread ignorance prevail. This is due in part to the complexity of the subject, but more to the fact that in the past no clear-cut methods of attacking the manifold problems involved had been devised. Happily this difficulty has at least in part been overcome.

It is no exaggeration to say that during the last fifteen years we have made more progress in measuring the extent of inheritance and in determining its elemental factors than in all previous time. Instead of dealing wholly now with vague general impressions and speculations, certain definite principles of genetic transmission have been disclosed. And since it is becoming more and more apparent that these hold for man as well as for plants and animals in general, we can no longer ignore the social responsibilities which the new facts thrust upon us.

Since what a child becomes is determined so largely by its inborn capacities it is of the greatest importance that teachers and parents realize something of the nature of such aptitudes before they begin to awaken them. For education consists in large measure in applying the stimuli necessary to set going these potentialities and of affording opportunity for their expression. Of the good propensities, some will require merely the start, others will need to be fostered and coaxed into permanence through the stereotyping effects of proper habits; of the dangerous or bad, some must be kept dormant by preventing improper stimulation, others repressed by the cultivation of inhibitive tendencies, and yet others smothered or excluded by filling their

PREFACE TO THE FIRST EDITION

place with desirable traits before they themselves come into expression.

We must see clearly, furthermore, that even the best of pedagogy and parental training has obvious limits. Once grasp the truth that a child's fate in life is frequently decided long before birth, and that no amount of food or hospital service or culture or tears will ever wholly make good the deficiencies of bad "blood," or in the language of the biologist, a faulty germ-plasm, and the conviction must surely be borne home to the intelligent members of society that one thing of superlative importance in life is the making of a wise choice of a marriage mate on the one hand, and the prevention of parenthood to the obviously unfit on the other.

In the present volume it is intended to examine into the natural endowment of the child. And since full comprehension of it requires some understanding of the nature of the physical mechanism by which hereditary traits are handed on from generation to generation, a small amount of space is given to this phase. Then, that the reader may appreciate to their fullest extent the facts gathered concerning man, a review of the more significant principles of genetics as revealed through experiments in breeding plants and animals has been undertaken. The main applications of these principles to man is pointed out in a general discussion of human heredity. Finally, inasmuch as, all available data indicate that the fate of our very civilization hangs on the issue, the work concludes with an account of the new science of eugenics which is striving for the betterment of the race by determining and promulgating the laws of human inheritance so that mankind may intelligently go about conserving good and repressing bad human stocks.

In order to eliminate as many errors as possible and avoid oversights I have submitted various chapters to certain of my colleagues and friends who are authorities in the special field treated therein. While these gentlemen are in no way responsible for the material of any chapter they have added greatly to the value of the whole by their suggestions and comments. Thus I am indebted to Professor Leon J. Cole for reading the entire manuscript; to Professors A. S. Pearse and F. C. Sharp for reading Chapter VII*; to Professor C. R. Bardeen for reading special parts; to Doctor J. S. Evans for reading Chapter VI

* Chapter numbers in this preface refer to first edition only.

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and part of V; to Doctor W. F. Lorenz, of the Mendota Hospital, for reading Chapter VIII; to Judge E. Ray Stevens for reading Chapter IX, and to Helen M. Guyer for several readings of the entire manuscript.

Grateful acknowledgment is made to all of these readers, to various publishers and periodicals for the use of certain of the illustrations, to the authors of the numerous books and papers from which much of the material in such a work as this must necessarily be selected, and to my artist, Miss H. J. Wakeman, for her painstaking endeavors to make her work conform to my ideas of what each diagram should show.

M. F. G.

PREFACE TO THE SECOND EDITION

Eleven years have elapsed since the first edition of this book was published. In the meantime knowledge in the field of genetics has advanced with such rapidity that a thorough revision and expansion of the entire book has become imperative. The wide and friendly interest shown by the public in the first edition has encouraged me in the belief that a further elucidation of some of the questions and the introduction of much new material will be welcomed. The sections on the physical basis of inheritance and on genetics proper have been greatly extended and separate chapters on embryology, the mechanics of development, immigration and population have been added. Numerous additions have been made to the chapter on human inheritance. Although some of the new material is more technical than most of that in the first edition, I have striven to maintain the same simplicity of presentation there employed, so that those with no previous knowledge of biology may continue to read it without undue difficulty.

I am indebted to Professor Royal H. Brink for a careful scrutiny of the material on biometry, to Professor Frederick L. Hisaw, that on embryology, and to Helen M. Guyer for critical reading of the entire manuscript. Grateful acknowledgment is also made to various publishers, periodicals and authors for the use of certain illustrations and much material.

M. F. G.

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BEING WELL-BORN

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CHAPTER I

HEREDITY

"My gifts have come to me from down the years:
I am the son of huntsmen of old time,
The heir of timid virtue and of crime,
Offspring of sluggards and of pioneers,
Inheritor of juggled hopes and fears.
Some gave me purity, some gave the grime
Of damaged souls. Some of them helped me climb
Toward God. From some came smiles, from others tears."
—BARKER.

It is a commonplace fact that offspring tend to resemble their parents. So commonplace, indeed, that few stop to wonder at it. No one misunderstands us when we say that such and such a young man is "a chip off the old block," for that is simply an emphatic way of stating that he resembles one or the other of his parents. The same is true of such familiar expressions as "what's bred in the bone," "blood will tell," and kindred phrases. All are but recognitions of the fact that offspring exhibit various characteristics similar to those of their progenitors.

Blood Heritage.—To this phenomenon of resemblance in successive generations based on ancestry, the term heredity is applied. In man, for instance, there is a marked tendency toward the reappearance in offspring of structures, habits, features, and even personal mannerisms, minute physical defects, and intimate mental peculiarities like those of parents or more remote forebears. These personal characteristics based on descent from a common source are what we may call the blood or, more accurately, the biological heritage of the child to discriminate it from a wholly different kind of inheritance, namely, the passing on from one generation to the next of such material things as per-

sonal property or real estate. The science concerned with heredity and the origin of individuals, or of new types of individuals, is called *genetics*.

Kind Determined by Origin.—It is inheritance in the sense of community of origin that determines whether a particular living creature shall be man, beast, bird, fish, or what not. A given individual is human because his ancestors were human. In addition to this supply of human qualities he has certain well-marked features which we recognize as characteristics of race. That is, if he is of Anglo-Saxon or Italian or Mongolian parentage, naturally his various qualities will be Anglo-Saxon, Italian, or Mongolian. Still further, he has many distinctive features of mind and body that we recognize as family traits, and lastly, his personal characteristics such as designate him to us as Tom, Harry, or James must be added. The latter would include such minutiae as size and shape of ears, nose or hands; complexion; perhaps even certain defects; voice; color of eyes; and many other particulars. Although we designate these manifold items as individual, they are in reality largely more or less duplicates of similar features that occur in one or the other of his progenitors, features which he would not have in their existing form but for the hereditary relation between him and them.

"Oh Damsel Dorothy! Dorothy Q.!

Strange is the gift that I owe to you;

What if a hundred years ago

Those close-shut lips had answered 'No,'

Should I be I, or would it be

One-tenth another, to nine-tenths me!"

"Soft is the breath of a maiden's yes;

Not the light gossamer stirs with less;

But never a cable that holds so fast

Through all the battles of wave and blast,

And never an echo of speech or song

That lives in the babbling air so long!

There were tones in the voice that whispered then

You may hear to-day in a hundred men."

When life steps into the world of matter there comes with it a sort of physical immortality, so to speak; not of the individual, it is true, but of the race. The important thing to note, however, is that the race is made up, not of a succession of wholly unrelated forms, but a continuation of the same kind of living organisms, and this sameness is due to the actual physical descent of each new individual from a predecessor. In other words, any living thing is the kind of organism it is in virtue of its hereditary relation to its ancestors.

It is part of the biologist's task to seek a material basis, a continuity of actual substance, for this continuity of life and form between an organism and its offspring. Moreover, inasmuch as the offspring is never precisely similar to its progenitors he must determine also what qualities are susceptible of transmission and in what measure.

Ancestry a Network.—From the fact that each child has all of the ancestors of its mother as well as of its father, arises the great complications which are met with in determining the lineage of an individual. A person has two parents, four grandparents, eight great grandparents, and thus following out pedigree it is plain to be seen that through this process of doubling in each generation, in the course of a few centuries one's ancestry is apparently enormous. By actual computation, according to Professor D. S. Jordan, if we count thirty generations back to the Norman invasion of England in 1066, at this ratio of duplication, the child of to-day would have had at that time an ancestry of 8,598,094,592 persons. But we know that the total number of inhabitants in the whole world—much less in England—has never been more than a fraction of this enormous aggregate. This means that we shall have to modify our inference that a child has twice as many ancestors as its parents; a condition which at first sight seems evident, but which is not literally true. The fact is that the parents of the child, in all probability, have many ancestors in common—a state of affairs which is brought about through the intermarriage of relatives, and this is especially frequent among remoter descendants of common progenitors. Time after time in genealogy strains of blood have crossed and recrossed, thus reducing the theoretical number of ancestors. Professor Jordan thinks it not improbable that a man of to-day who is of English origin has blood in his veins from practically every inhabitant of England who

lived during the time of William the Conqueror and who left fruitful descendants; and Professor C. B. Davenport concludes that at the present time all people of English descent are related to within the degree of thirtieth cousins, at least, and that most of them are even more closely related. Some genealogists are inclined to doubt this, however, on the ground that because of the tendency toward selective or assortative mating certain strains have not intermingled extensively with others. Instead of conceiving of ancestry as an ever branching and widening tree-like system as it recedes into the past, it is more accurate, then, to regard it in the light of an elaborate meshwork. The "family tree" in reality becomes the family net.

Ancestry in Royalty.—The pedigrees of royal families have proved to be of much importance in the study of human inheritance, not that royal traits are any more heritable than any other, but simply because the records have been carefully kept so that they are the most comprehensive and easily followed pedigrees available. The net-like weave of ancestry is particularly well exemplified in some of these families because of much close intermarriage. Their heritage typifies on an intensified scale the heritage of the mass of mankind. For example, if we go six generations back in the ancestry of Frederick the Great, instead of the expected 64 individual ancestors we find only forty; or in a still more closely-woven stock, in the Spanish royal line of Don Carlos we find in six generations instead of 64 individual ancestors, only 28. If no individual appeared more than once in his ancestry, the present Prince of Wales would have had 4,096 separate ancestors in the twelfth generation back, but according to a recent study made by Mrs. O. A. Merritt Hawkes, 2,997 persons appear more than once, there are 766 unknown ancestors, and only 333 who are known not to have appeared before.

Offspring Derived from One Parent Only.—So far in our reckoning of heredity we have counted elements from father and from mother, and the complications which arise from such a double ancestry are manifestly very perplexing ones. If we could do away with one sex and find offspring that are derived from one parent only, it would seemingly simplify our problem very much for we should thus have a direct line of descent, free from intermingling. This, in fact, occurs to a greater or less extent in a number of instances among lower animals. There

may be only female forms for a number of generations and the eggs which they produce develop directly into new individuals. Moreover, many of the simpler organisms have the power of dividing their bodies and thus giving rise to two new forms, each of which resembles the parent. This shows plainly that we may have inheritance without the appearance of any male ancestor at all, hence sex is not always a necessary factor in reproduction or heredity. The development of eggs asexually, that is, without uniting first with a male cognate, is termed *parthenogenesis*. The ordinary plant louse or aphid which is frequently found upon geraniums is a familiar example of an animal which reproduces largely in this way. During the summer only the females exist and they are so astonishingly fertile that one such aphid and her progeny, supposing none dies, will produce one hundred million in the course of five generations. In the last broods of the fall, males and females appear and fertile eggs are produced which lie dormant through the winter to start the cycle of the next year. Again, the eggs of some kinds of animals which normally have to unite with a male germ before they develop, can be made to develop by merely treating them with some one of various chemical agents or even by physical means. The difference between an offspring derived in such a manner, and one which has developed from an egg fertilized by the male is that it is made up of characteristics from only one source, the maternal.

Dual Ancestry an Aid in Studying Heredity.—Although we have the factors of heredity in a more simplified form in the case of asexual transmission, as a matter of fact most of our insight into the problems of heredity has been attained from a study of sexually reproducing forms, because the very existence of two sets of more or less parallel features offers a kind of checking up system by which we can follow a given characteristic.

Reversion.—Occasionally, however, plants and animals do not develop the individuality we might expect, but stop short at or re-attain some ancestral stage along the line of descent, and thus come to resemble some progenitor perhaps many generations back of their own time. Thus it is well known that a child may resemble a grandparent or remote ancestor much more closely than its immediate parent. The reappearance of such ancestral traits the student of heredity designates as *reversion* or *atavism*.

Reversion may occur apparently in any kind of plant or animal. It is especially pronounced among domesticated forms, which through man's selection have been produced under more or less artificial conditions. For example, among fancy breeds of pigeons, there may be an occasional return to the old slate-blue color of the ancestral rock-pigeon, with two dark cross-bars or black checkering on the wings, from which all modern breeds have been derived. This is almost sure to happen if different fancy varieties are intercrossed for two or three generations. Another example of reversion frequently cited is the occasional reappearance in domestic poultry of the reddish or brownish color pattern of the ancestral jungle-fowl to which, among modern forms, the Indian game seems most nearly related in color. Still another example is the crossbars or stripes occasionally to be seen on the forelegs of colts, particularly mules, reminiscent of the extinct wild progenitors which were supposedly striped.

Fig. 1, opposite, is a picture of a hybrid between the common fowl and the guinea-fowl. The chevron-like markings on certain feathers show a reversion to a type of color pattern that is prevalent among both the primitive pheasants (the domestic chicken is a pheasant) and the primitive guinea-fowls. Although the common spotted guinea-fowl may be crossed with a black chicken which shows no trace of barring, nevertheless, the hybrid offspring are likely to bear a chevron-like pattern such as that shown in the picture.

There has been much quibbling over the relative meanings of reversion and atavism. The general idea, whichever term we use, is that there is a "throwing back" in a noticeable degree through inheritance to some ancestral condition beyond the immediate parents. A few recent authors have taken the term atavism in a restricted sense and use it to signify specifically those not uncommon cases in which a particular character of an offspring resembles the corresponding character of a grandparent instead of a parent. Such, for example, as the blue eye-color of a child with brown-eyed parents, each of whom in turn has had a blue-eyed parent. The tendency of other authors is to abandon the term entirely because of the diversity of meaning that has been attached to it in the past.

Certain classes of so-called reversions, such as the case of the eye-color just cited, are readily explicable on Mendelian prin-



FIG. 1. Hybrid between the guinea-fowl and the common fowl, showing in many feathers reversion to a primitive chevron-like barring.

ciples as we shall see in a later chapter, but probably not all kinds of phenomena described as reversion can be so explained. For example, some seem to be cases of suppressed development. The word reversion, indeed, must be looked on as a convenient descriptive term rather than as the name of a single specific condition.

Three Types of Reversion.—At least three fairly distinct types of phenomena often designated as reversion are recognizable: (1) recombination of characters—or rather, of the factors of characters—which became separated in some way in previous generations; (2) removal of superimposed or obscuring factors; and (3) arrested development.

The first type is well exemplified by the results obtained from crossing various strains of the cultivated sweet pea. White varieties are known, for example, which when crossed one with another produce plants that bear colored flowers similar in appearance to the blossom of the wild Sicilian sweet pea, the probable ancestor of our present cultivated forms. In such cases the color characteristic of the original wild species is evidently due to the interaction of two or more factors. In the white strains these have become separated so that any particular white variety has an incomplete set and therefore can not produce color. When, however, such a strain is crossed with another that contains the missing factor or factors the color is restored. Cases of this kind are known not only in plants but among animals as well. For example, crosses between albino mice and black mice often result in reversions to the wild gray color, or various true-breeding forms of fancy rabbits when cross-bred frequently bear young of the characteristic grayish type, known as *agouti*, seen in the coat-color of our common wild “cotton-tail” rabbit.

In the simplest cases only two factors are concerned and one is brought in from each parent. In other cases, however, a number of factors are involved, different combinations of which may produce different effects. In the sweet pea, for example, six different color forms in addition to white are known. Similarly the gray coat of the rabbit depends upon at least five different factors. To get a complete “reversion” to the ancestral type, therefore, the reverting individual must contain a full set of all the separate color factors present in the original wild form.

As regards reversionary phenomena based on the removal of

obscuring factors, innumerable instances might be cited, such as the reappearance of albinos among the offspring of parents who though non-albinic themselves are of albinic origin; or, to take a more familiar illustration, the reappearance of blue eyes in the children of two brown-eyed parents each of whom had a blue-eyed ancestor. In the latter case, the fact is that in man blue is common to all pigmented eyes. Individuals with brown or black eyes have in addition to the blue a brown-pigment-forming factor which usually, shortly after birth, becomes active and leads to the formation of a dark pigment that veils or obscures the blue. This factor is independently transmissible, in a manner to be explained later. When it is absent the blue is visible, but when present, brown or black eyes result.

Examples of the type of so-called reversion attributable to suppressed development are such monstrosities as: the occasional appearance of a two- or three-toed colt, in horses; tailed human beings, hairy human freaks; human individuals with supernumerary breasts or nipples; harelip or cleftpalate; and various other anomalies which will be discussed more fully in the chapter on embryonic development.

There is no doubt that in an earlier stage of evolution, well attested by fossil remains, the ancestors of modern horses were three-toed; the small pair of "splint" bones adhering to the so-called cannon bone (the third metacarpal or metatarsal) of the modern horse are unquestionably vestiges of such extra toes. Occasionally stimuli of unknown origin stir such slumbering rudiments into renewed activities which result in the partial or complete reappearance of this earlier ancestral three-toed condition. As to the origin of an occasional tailed human being, a study of human embryology reveals that at one stage of development the human embryo, presumably reminiscent of a tailed ancestry, possesses a definite tail-like extension. Ordinarily this disappears but cases are on record where failure to do so has resulted in the birth of a tailed child. Again, the entire body of the human fetus except the palms and soles is, for a time, covered with a coat of fine downy hair termed the *lanugo*, supposedly indicative that the earlier ancestors of man had well-haired bodies. This covering usually disappears before birth but exceptionally it may persist permanently on face or body, giving rise to such individuals as the "dog-faced" men of side-show fame. The other anomalies mentioned likewise correspond

structurally to fully developed functional parts in certain of the lower vertebrates, but in man they represent the stoppage of the development of such a part at an early stage—presumably a lower ancestral level—which should normally be passed through but which should not persist.

Telegony.—There is yet a wide-spread belief in the supposed influence of an earlier sire on offspring born by the same mother to a later and different sire. This alleged phenomenon is termed *telegony*. For example, many dog-breeders assert that if a thoroughbred bitch has ever had pups by a mongrel father, her later offspring, although sired by a thoroughbred, will show taints of the former mongrel mating. In such cases the female is believed to be ruined for breeding purposes. Other supposed instances of such influences have been cited among horses, cattle, sheep, pigs, cats, birds, pets of various kinds and even men. The historic case most frequently quoted is that of Lord Morton's mare which bore a hybrid colt when bred to a quagga, a striped zebra-like animal now extinct. In later years the same mare bore two colts, sired by a black Arabian horse. Both colts showed stripes on the neck and other parts of the body, particularly on the legs. It was inferred that this striping was a sort of after effect of the earlier breeding with the quagga. In recent years, however, Professor Ewart has repeated the experiment a number of times with different mares using a Burchell zebra as the test sire. Although his experiments have been devised so as to conduce in every way possible to telegony his results have been negative. Moreover, it has been pointed out that the stripes on the legs of the two foals alleged to show telegony could not have been derived from the quagga sire for, unlike zebras, quaggas did not have their legs striped. Furthermore it is known that the occurrence of dark brown stripes on the neck, withers and legs of ordinary colts is not uncommon, some cases of which have exhibited more zebra-like markings than those of the colts from Lord Morton's mare. It seems much more probable, therefore, that the alleged instances are merely cases of ordinary reversion to the striped ancestral color pattern which probably characterized the wild progenitors of the domesticated horse.

Various experiments on guinea-pigs, horses, mice and other forms, especially devised to test out this alleged after-influence of an earlier sire, have all proved negative and the general belief of the biologist to-day is that telegony is a myth.

Prenatal Influences Apart from Heredity.—In discussing the problems of heredity it is necessary to consider also the possibilities of external influences apart from lineage which may affect offspring through either parent. Although modifications derived directly by the parent, and prenatal influences in general, are of extremely doubtful value as of permanent inheritable significance, nevertheless they must be reckoned with in any inventory of a child's endowment at birth. Impaired vitality on the part of the mother, bad nutrition and physical vicissitudes of various kinds all enter as factors in the birthright of the child, who, moreover, may bear in its veins slumbering ills from some progenitor who has handed on blood taints not properly attributable to heredity. Of such importance is this kind of influence to the welfare of the immediate child that it will be necessary to discuss it in considerable detail in a later chapter.

Parent Body and Germ Not Identical.—Inasmuch as each new individual appears to arise from material derived from its parent, taking the evidence at its face value one might suppose that any peculiarity of organization called forth in the living substance of the parent would naturally be repeated in the offspring, but a closer study of the developing organism from its first inception to maturity shows this to be probably a wrong conclusion. The parent body and the reproductive substance contained in that body are by no means identical. It becomes an important question to decide, in fact, how much effect, if any, either permanent or temporary, the parent body really has on the germ.

A given fertile germ (Fig. 2, p. 11) gives rise by a succession of divisions to a body which we call the individual, but such a germ also gives rise to a series of new germ-cells which reside in that individual, and it is these germ-cells, not something derived from the body, that pass on the determiners of distinguishing features or qualities from generation to generation. It is only by grasping the significance of this fact that we can understand how in certain cases a totally different set of characters may appear in an offspring than those manifested in either parent. In sexual reproduction, of course, the germplasms of two individuals unite into a common mass to constitute the new organism.

An Hereditary Character Defined.—By a *character*, in discussions in heredity, is meant simply a trait, feature or other

characteristic of an organism. Where we can pick out a single definable characteristic which acts as a unit in heredity, for greater accuracy we term it a *unit-character*. Many traits are known to be inherited on a unit basis or are capable of being analyzed into factors which are so inherited. These unit-characters are in large measure inherited independently, or as unitary groups which are independent of one another.

Hereditary Mingling a Mosaic Rather Than a Blend.—The independence of unit-characters in inheritance leads us to the important conclusion that the mingling of two lines of ancestry into a new individual is in no sense bringing them into the “melting pot,” as it has been picturesquely expressed, but it is

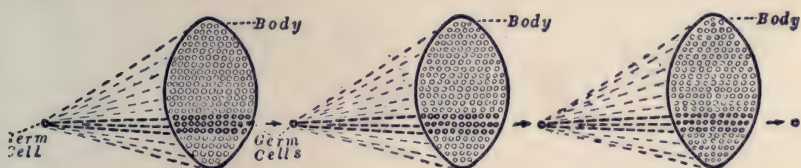


FIG. 2

Diagram illustrating germinal continuity. Through a series of divisions a germ-cell gives rise to a body or soma and to new germ-cells. The latter, not the body, give rise in turn to the next generation.

rather to be regarded as the mingling of two mosaics, each particle of which retains its own individuality, and which, even if overshadowed in a given generation, may nevertheless manifest its qualities undimmed in later generations when conditions favorable to its expression transpire.

Determiners of Characters, Not Characters Themselves, Transmitted.—The fact should be thoroughly understood that the actual thing which is transmitted by means of the germ in inheritance is not the character itself, but something which will *determine* the character in the offspring.

Any differential cause in a germ-cell which is instrumental in establishing a particular attribute of a part or of an organism is called the *determiner*, *gene* or *factor* of that attribute. The attribute itself constitutes what has been termed a unit-character. Individual genes, however, are not to be regarded as exclusive units upon which alone a character depends. They are co-operants, not monopolists, since unquestionably, from the very relatedness of the parts of an organism, any particular

feature necessarily requires more than a single germinal element to bring it into expression. Conversely, any single germinal constituent may condition more than one character. Materially considered a gene is merely a chemical substance which performs a definite function in the establishment of one or more parts or traits of an organism. Modify or remove it, and a change of some kind, visible or invisible, results in the corresponding part. We think of a single gene as identified with any unit-character only in so far as, in our genetical analysis, we find unitary modifications in the body can be referred to single factor-differences in the germ. The germinal single factor-differences are the real things back of the unit differences we discuss in heredity. It is important to remember this, for often these *determiners* or *genes* may lie unexpressed for one or more generations and thus become manifest only in later descendants. The truth of the matter is, the child does not inherit its character from corresponding characters in the parent body, but parent and child are alike because they are both products of the same line of germplasm, both are chips from the same old block.

CHAPTER II

METHODS OF STUDYING HEREDITY

Before entering into details it will be well to get some idea of the methods which are commonly employed in arriving at conclusions in the field of genetics. Some of these are extremely complex and all that we can do in an elementary presentation is to glimpse the procedures.

Our Knowledge of Heredity Derived along Three Lines.—

Our modern conceptions of heredity have been derived mainly from three distinct lines of investigation: First, from the study of embryology, in which the biologist concerns himself with the genesis of the various parts of the individual, and the mechanism of the germs which convey the actual materials from which these parts spring; second, through experimental breeding of plants and animals to compare particular traits or features in successive generations; and third, through the statistical treatment of observations or measurements of a large number of parents and their offspring with reference to a given characteristic in order to determine the average extent of resemblance between parents and children in that particular respect.

The Method of Embryology.—Living organisms invariably arise as the offspring of preexisting living organisms of the same kind. Since a newly produced individual usually closely resembles or grows to resemble the parent form, we speak of the process by which it comes into being as *reproduction*. The fact should be clearly recognized, however, that the egg which is the initial form of the new being is not a thing apart which by some form of natural necromancy *becomes* an individual, but that it *is* an individual from the outset—only, an individual in a less developed or specialized condition than the adult organism. The gap between egg and adult is bridged by a long series of structural and functional changes through which the complexity of the adult gradually emerges. The finished product is only a more elaborate expression of the new individual that originally entered upon the series of transformations known as development.

The facts regarding the formation of germ-cells and the subsequent processes of development which begin with fertilization of the egg, constitute the science of *embryology*. Not infrequently, however, the study of the genesis and behavior of the germs, fertilization, and the initial stages of body-building are regarded as belonging to the science of cellular biology called *cytology*, and the term *embryology* is restricted more exclusively to the genesis of the body.

Inasmuch as the egg no less than the adult is an individual, and since this is also true of all intervening stages of development, to get a true conception of heredity we must think of it as resemblance of offspring to progenitors at all corresponding stages of development.

The student of *embryology* is working with the very material out of which the so-called hereditary characters are built. Anything he learns concerning how such characters come into being in the individual, therefore, must necessarily shed light upon their reappearances in successive generations. The *embryologist* finds that the characteristics of the later stages of development are contingent on the earlier ones and ultimately on the constitution of the fertile egg, and that development is really a series of reactions, one condition leading to the next. He is in position, furthermore, to appraise the relative importance of in-born constitution and of external factors, not only through observation of normal development but by experimental alteration of either external or internal conditions. Through experimental *embryology* and the broader science of experimental morphology, indeed, many astonishing facts have been learned regarding the mechanism and processes which underlie development and hence also of the things developed—the hereditary traits.

The Method of Experimental Breeding.—A tremendous impetus was given to the method of experimental breeding when it was realized that we can itemize many of the parts or traits of an organism into entities which are inherited independently one of another. Such traits, or as we have already termed them, unit-characters, may be not only independently heritable but independently variable as well. The experimental method seeks to isolate and trace through successive generations the separate factors which determine the individual unit-characters of the organism. In this attempt cross-breeding is resorted to. Forms which differ in one or more respects are mated and the progeny

studied. Next these offspring are mated with others of their own kind or mated back with the respective parent types. In this way the behavior of a particular character may often be followed and the germinal constitutions of the individuals concerned can be formulated with reference to it. Inasmuch as we shall give much consideration to this method in the chapters on Mendelism we need not consider it further here.

The Statistical Method.—The statistical method seeks to obtain large bodies of facts and to deal with evidence as it appears through mathematical analysis of these facts. The attempt of its followers is to treat quantitatively all biological processes with which it is concerned. Historically Sir Francis Galton was the first to make any considerable application of statistical methods to the problems of heredity and variation. In his attempts to determine the extent of resemblance between relatives of different degree as regards bodily, mental and temperamental traits, he devised new methods of statistical analysis which constitute the basis of modern statistical biology, or *biometry* as it is termed by its votaries. Professor Karl Pearson in particular has extended and perfected the mathematical methods of this field and stands to-day as perhaps its most representative exponent. Prominent American biometrists are Professor Raymond Pearl and Professor J. Arthur Harris. The biometrical system is in the main based on the calculus of probability. The methods often are highly specialized, requiring the use of higher mathematics, and are therefore only at the command of specially trained workers.

Just as insurance companies can tell us the probable length of human life in a given social group, since although uncertain in any particular case, it is reducible in mass to a predictable constant, so the biometrician with even greater precision because of his improved methods can often, when a large number of cases are concerned, give us the intensity of ancestral influence with reference to particular characters.

For example, it is clear that by measuring a large number of adult human beings one can compute the average height or determine the height which will fit the greatest number. There will be some individuals below and some above it, but the greater the divergence from this standard height the fewer will be the individuals concerned.

Galton compared the heights of 204 normal English parents

and their 928 adult offspring. In order to equalize the measurements of men and women he found he had to multiply each female height by 1.08. Then, to take both parents into account when comparing height of parents with that of children he added the height of the father to the proportionately augmented height of the mother and divided by two, thus securing the height of what he termed the "mid-parent." He found that the mid-parental heights of his subjects ranged from 64.5 to 72.5 inches, and that the general *mode* was about 68.5 inches. It should be mentioned that the *mode*, in a given population, represents the group containing the largest number of individuals of one kind; it may or may not coincide with the average. The children of all mid-parents having a given height were measured next and tabulated with reference to these mid-parents. The results of Galton's measurements may be expressed simply as follows:

	MODE									
Height of mid-parent in inches....	64.5	65.5	66.5	67.5	68.5	69.5	70.5	71.5	72.5	
Average height of offspring.....	65.8	66.7	67.2	67.6	68.3	68.9	69.5	69.9	72.2	

The Law of Regression.—It is plain from this table that the offspring of short mid-parents tend to be under average or modal height though not so far below as their parents. Likewise, children of tall parents tend to be tall but less tall than their parents. This fact illustrates what is known as Galton's *law of regression*; namely, that if parents in a given population diverge a certain amount from the mode of the population as a whole, their children, while tending to resemble them, will diverge less from this mode. In other words, the drag of a miscellaneous ancestry causes regression from the exceptional parent toward the mode of the stock. It is clear that the extent of regression is an inverse measure of the intensity of inheritance from the immediate parents; if the deviation of the offspring from the general mode were nearly as great as that of their parents then the intensity of the inheritance must be high; if but slight—that is, if the offspring regressed nearly to the mode—then the intensity of the inheritance must be ranked as low. In the example in question it must be ranked as relatively high. Computations show that as regards stature the fraction two-thirds represents approximately the amount of resemblance between the two generations where both parents are considered.

The Law of Probability.—The so-called “law of probability” is the fundamental principle around which biometrical investigations revolve. According to this law, if, under constant conditions, any one of certain different events is equally likely to happen, then, if all are repeatedly given sufficient opportunity to occur, each will happen with equal average frequency. In tossing a coin repeatedly, for example, in the long run the chance is that one will throw approximately as many “heads” as “tails.” Or, supposing one wanted to get some knowledge of the height of men in a college numbering one thousand men, if he obtained the average height of one hundred of these men chosen *at random*, the chances are that this figure would be a fair indication of the average height of the student body as a whole. The probability of accuracy would increase, of course, if a still greater proportion of the students were measured. Since it is usually impossible to measure or study every individual of a very large group, this principle of “random sampling” is frequently resorted to in statistical studies. It is obvious that to get a fair sample it must be sufficiently large and be unselected.

Frequency Polygons.—In determining such averages, however, it quickly becomes apparent that in individual cases we may have considerable deviation from the commonest type, both above and below it, and it becomes a matter of importance to know what the extreme limits are, what proportion of individuals reach these limits, and how many individuals fall in each group or class of intergrades we can conveniently make between the mean and the extremes. The *mean* or *average* is found by multiplying the number of individuals in each class by the value of that class, adding all the products thus obtained, and dividing by the total number of individuals. In measuring height, centimeters or inches are commonly used as the unit for grouping individuals into classes, each person being placed in that class within the limits of which he falls. Thus, Fig. 3, p. 18, represents graphically such a series of classified measurements of stature made by Pearson upon 1,052 English mothers. The upper row of numerals indicates relative heights in inches. The lower row gives the number of mothers found in each class—that is, of the same height to the nearest inch, while the vertical columns represent by their proportional heights these same numbers in the form of a graph so that one can see at a glance the relative proportions of individuals in each group or class. The

heights ranged from 54 to 71 inches. The most frequent height—in other words the *mode*—was between 62 and 63 inches. In the case of height, there are all intergrades between the extremes, the number of classes above and below the *mode* are equal and the number of individuals (called *variates*) in each class falls steadily and in approximately the same degree toward the extremes. A line drawn joining the mid-points of the tops of the several columns gives what is called a *frequency curve*. When a sufficiently large number of individuals has been used

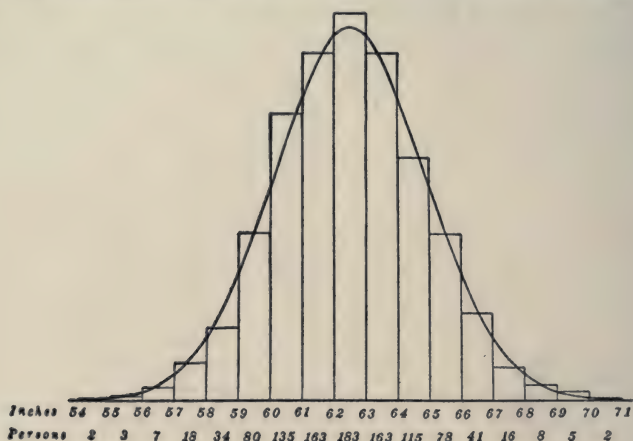


FIG. 3

Recorded measurements of the stature of 1,052 mothers. The height of each rectangle is proportional to the number of individuals of each given height. The curve connecting the tops of the rectangles is the normal frequency curve. The most frequent height is between 62 and 63 inches. Average height—62.5 inches. Standard deviation, 2.39 inches. Coefficient of variability, 3.8 ($2.39 = 3.8\%$ of 62.5 inches). (From Pearson.)

in the sample measured, such a curve gives us a picture (or *frequency polygon*) of the degree and extent of variability of a given character in a particular group. The curve of variation for height approaches closely the ideal “curve of chance” or “curve of probability” of the mathematician. This theoretical, symmetrical curve is also called by mathematicians a “frequency of error curve,” the “normal frequency curve,” or simply a “normal curve.” In the normal curve the *mode* coincides with the *mean*.

The Normal Frequency Curve.—The normal curve is the form assumed by the distribution of any differences that are governed wholly by chance—which means that any particular fluctuation in any given individual is really the result of the operation of a multiplicity of factors or causes acting in the one direction as often as in the other. The curve is called a theoretical one because actually whatever we were measuring or estimating would have to be scaled into a limited number of “classes,” and it is the tops of the successive columns of graded heights

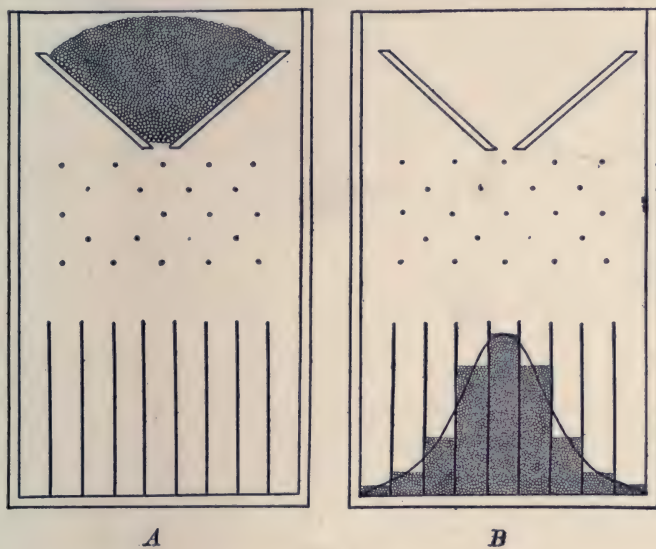


FIG. 4

Model to illustrate the law of probability or “chance.” Description in the text. *A*, shot held in container at top of board. *B*, shot after having fallen through the obstructions into the vertical compartments below. The curve connecting the tops of the columns of shot is the normal probability curve.

indicating these classes that determine the curve. Instead of an actual smooth curve there is really, then, only a stepped pyramidal effect. The greater the number of classes the smaller the steps become but mathematically considered it would require an infinite number of classes to make the steps disappear entirely, leaving a perfectly smooth curve which would indicate an absolutely continuous distribution.

Certain of the facts of chance variability may be shown, as

suggested by Galton, by a simple modification of the bagatelle board (Fig. 4). Below the funnel-shaped container which is filled with shot, peas or similar round smooth objects (Fig. 4, A), a series of symmetrically arranged pins or nails is placed to act as obstacles. Underneath these and symmetrically spaced with reference to them is a row of compartments of equal size. When the shot are permitted to fall from the container through the field of obstacles into the compartments below (Fig. 4, B), they are distributed according to the "law of chance." If the apparatus has been accurately constructed their distribution is such that a curve connecting the tops of the columns closely approximates the *normal frequency curve*. No matter how often the operation is repeated approximately the same type of distribution will occur, so that we can safely predict in advance that the middle compartment will receive the most, those next to it fewer, and those increasingly distant, still fewer. But it is quite evident also that, although we know in advance with fair accuracy what the general distribution of the objects will be, we can not predict with certainty what the future position of any particular one of the objects will be. We can only say that it is most likely to fall into the middle compartment, or that the probability that it will fall into either one of the outermost compartments is slight. The chances that it will fall to the right or the left of the middle compartment are equal. Thus it is evident that in such a purely chance distribution there will always be many more individuals near the mean than near the extremes and that the number of individuals in a class becomes increasingly fewer as the class is farther removed from the mean.

Data Required for Correct Knowledge of a Group.—It is clear, moreover, from such a model that where, in a group of individuals, the point at issue is the degree of expression of a certain part or other characteristic, the most representative condition will be found in the individuals nearest the mean, that an individual taken from one or the other of the extremes would not represent the whole group fairly. To get a correct idea of a group, therefore, we must know: (1) the extent of deviation there may be in each direction from the mean; (2) whether or not the majority of the classes arranged according to our unit of measurement stand close to the mean or are widely scattered (shown by whether the curve is narrow and tall or broad and flat); and (3) whether the deviations are symmetrically related

to the mean, as in the normal curve, or whether variations tend more toward one extreme than toward the other with the result that the curve becomes unsymmetrical or skew with a steep slope on one side and a more gradual one on the other, or even more complex with more than one peak.

It is to express such facts as these that statisticians have devised various special mathematical formulas. While these often have a forbidding appearance to the ordinary reader because of his unfamiliarity with mathematical symbols, as a matter of fact the ideas or facts back of them are not hard to understand. (See Appendix A.)

The Principle of Correlation.—In studies in inheritance the thing of primary interest is not merely the range of variation of some feature in a given group but rather how offspring compare in this particular with their forebears. For the purpose of showing the extent to which a given character stands in agreement with its expression in an earlier generation the biometrician makes use of what is termed the *coefficient of correlation*. When one specific thing or activity varies and another one varies in agreement with it, the two are said to be *correlated*. Degree of correlation is conventionally expressed on a scale running from -1 through 0 to 1 .

As a very simple and imaginary illustration in correlation one might select the problem of whether or not all great men are born in the country. If a study of the biography of many thousand celebrities revealed that every one of them had been born in the country, then the correlation between rural birth and greatness, for the group studied, would be complete (that is 1). But if it were found that all the celebrities in question had been born in cities or towns and not one in the country, then the reverse or negative correlation would be complete (that is -1). If it were found that just as many great men—no more, no less—were born in the country as in cities and towns, then the result would be expressed numerically by 0 . In other words there would be no correlation between greatness and rural birth. Obviously any preponderance of relationship between greatness and rural birth, or greatness and urban birth, is expressible as a plus or a minus decimal on either side of 0 varying from -1 to 1 .

In biometry two important uses are made of the principle of correlation: (1) to show whether or not certain characters are interdependent in a given organism; (2) to measure the

degree of resemblance of characters in successive generations. Knowledge of the facts in the first of these fields as well as in the second is of importance in genetical studies, for it is clear that if certain characters are so interrelated that when one varies the others are also affected, selection with reference to any one of these factors would have an effect upon the others.

Correlations in Human Families.—Using this principle of correlation as a standard, Pearson has found for the many physical and mental traits which he has measured that in general parent and child have a correlation of slightly less than 0.50, while the coefficient between brother and brother, sister and sister, or brother and sister was a trifle more than 0.50. Since, in spite of Galton's attempt to establish a hypothetical mid-parent there is no satisfactory method of determining in a single measurement the relation between children and both parents, it is obvious that information derived from the coefficient of correlation between child and parent is deficient in that it takes into account only one parent. The correlation with the other parent, though just as important, has to be determined separately.

Assortative Mating.—As an example of a correlation which is of significance in human matings may be mentioned the frequency with which a tall man tends to marry a woman of above average height. Pearson found by actual measurements that a man who exceeds the average male height by a given amount most frequently marries a woman who exceeds the average height for women by a little more than one-fourth as much as her husband exceeds the male average. This indicates more or less of a tendency toward *assortative mating*—the tendency of like to mate with like. Tendency toward assortative mating has been found for such diverse traits as eye-color, hair-color, intelligence, general health, insanity, congenital defects and longevity.

The Biometrical Method, Statistical, Not Physiological.—Statistical studies can tell us about the general occurrence and distribution of various traits, and thus, as it were, outline the problem for us, but they give little or no direct aid toward understanding the nature or causes of the phenomena in question. The chief danger in employing this method, unchecked by the experimental method and the intensive study of individual pedigrees, lies in the fact that resemblances which are being observed and measured may be due to very different causes. In studying heredity, for example, the measurement of differences or resemblances in the expression of a certain part or trait may be mis-

leading unless we have some means of discriminating between how much such expression is the result of inheritance, how much the outcome of environmental influence. To determine conclusively whether certain characters are truly hereditary or merely environmental one must test out the experimental animals or plants by, (1) varying the environment and observing whether or not the characters in question remain constant, and (2) by keeping the environment as uniform as possible and determining the range of expression of the traits under observation. When once the things to be compared are classified with reference to a common basis of causation, however, the biometrical method becomes a valuable aid. Even the experimental method must call on the statistical for the quantitative appraisal of its results.

While biometry may in certain cases go far toward showing us the average intensity of the inheritance of certain characters it can not replace the method of the experimental breeder which deals with particular characters in individual pedigrees. It must be borne in mind that the biometrical method is a statistical and not a physiological one and that it is applicable only when large numbers of individuals are considered in mass. It is most valuable in cases where we are unable sharply to define single characters, due probably to the concurrent action of a number of independent causes, or where experiment is impossible so that we have to depend solely on numerical data gained by observation.

Mental Qualities Inheritable.—Galton showed by this method long ago, and Pearson and his school have extended and more clearly established the work, that exceptional mental qualities tend to be inherited. While on the average the children of exceptional parents tend to be less exceptional than their parents, still they are far more likely to be exceptional than are the children of average parents. After making due allowance for environmental influences, it has been shown that such mental and temperamental attributes as ability, memory for numbers, vivacity, conscientiousness, industry, efficiency, attentiveness, perseverance and temper, are, like physical features, based on hereditary endowment.

For some of the more important methods and formulæ used in biometrical studies in heredity, the reader is referred to Appendix A. Intelligent combination of all methods—embryological, experimental, statistical—is necessary in modern genetics.

CHAPTER III

REPRODUCTION

Before we can make any detailed analysis of the inheritance of characters we should have some general idea of the physical structure of animals and particularly some familiarity with the development of an individual from the egg, as well as some knowledge of the nature of the germ-cells.

Reproduction Based on Metabolism.—The living substance of any organism, whether plant or animal, is called *protoplasm*. Habitually, when speaking of heredity, we think of the multifarious "characters" displayed by the developed individual as the things inherited, but what actually happens generation after generation is a reduplication of germinal protoplasm. It is characteristic of all living protoplasm that its very existence is but the expression of a state of approximate balance between constructive nutritive processes and destructive waste activities which are in ceaseless operation. The sum total of these chemical reactions which characterize living things is termed metabolism. It is distinctive of the living organism that the protoplasm of each tissue when broken down can select from the nutrient stream the particular ingredients it needs to reconstruct or repair its own peculiar substance. In other words, the nature of the materials into which food-units are combined is determined by the specific constitution of the tissues themselves. This is true no less of germinal than of somatic protoplasm.

When constructive exceed destructive activities, growth results, and one step beyond ordinary growth is that overgrowth which, as a detached individual, constitutes a newly *reproduced* organism. It is important to keep in mind that the protoplasmic substance of this new individual is but a continuation of the specific protoplasm peculiar to an earlier individual—or in sexual reproduction, to two individuals—and that inevitably, therefore, unless outside factors intervene, the anatomical and physiological complexities which arise through embryonic development must be similar to those of such predecessors. Reproduction, in other

words, is the passing on of metabolic activities already established.

The Cell the Unit of Structure.—If we examine one of the higher animals, as, for example, the horse, the dog, or man, we find that it is made up of a large number of constituents, such as bones, muscles, nervous elements, blood and other tissues. Each kind of tissue is composed of a number of living units, ordinarily microscopic in size, which are known as cells. A careful examination of various cells reveals that although they may differ greatly in size, shape and minor details, they all alike possess certain well-marked characteristics. Each when reduced to its fundamental form is seen to consist of a small mass of living matter termed protoplasm in which may usually be distinguished two regions—the cell-body, or *cytosome*, and the *nucleus* (Fig. 5, p. 26). Any cell, whether it be of the brain, of the liver, or from any organ of an animal or plant, has this same fundamental structure. In addition, a limiting membrane or wall of some kind is generally present, although it is not a necessary constituent of all cells.

Unicellular Organisms.—While such a structure as a tree or a horse is composed of countless millions of cells, on the other hand numerous organisms, both plant and animal, exist which consist of only one cell. Yet this cell is just as characteristically a cell as are the components of a complex animal or plant. It has the necessary parts, the cell body and the nucleus. Moreover, it exhibits all of the fundamental activities of life, though in a simplified form, that a complex higher organism does.

Importance of Cell Theory.—This discovery that every living thing is a single cell or an aggregation of cooperating cells and cell products is one of our most important biological generalizations because it has brought such a wide range of phenomena under a common point of view. In the first place, the structure of both plants and animals is reducible to a common fundamental unit of organization. Moreover, both physiological and pathological phenomena are more readily understood since we recognize that the functions of the body in health or disease are in large measure the result of the activities of the individual cells of the functioning part. Then again, the problems of embryological development have become much more sharply defined since it could be shown that the egg is a single cell and that it is through a series of divisions of this cell and subse-

quent changes in the new cells thus formed that the new organism is built up. And lastly, the problem of hereditary transmission

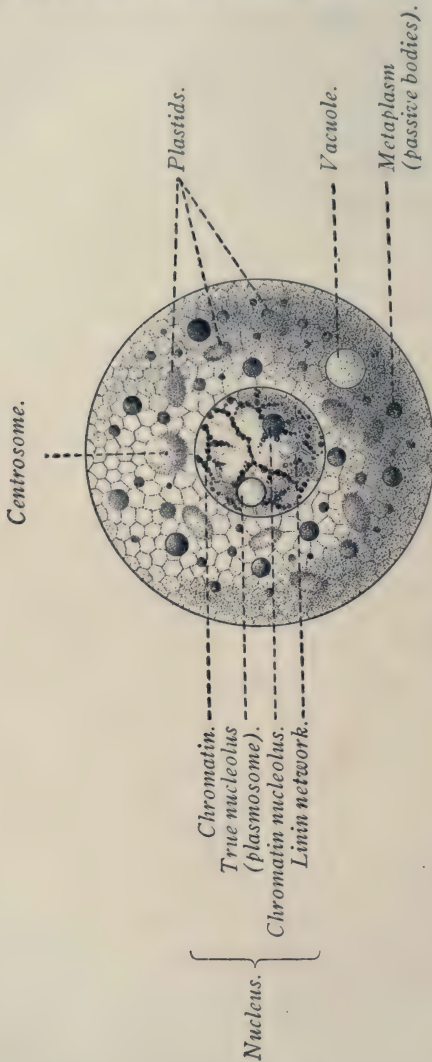


Fig. 5
Diagram of a cell showing various parts.

has been rendered more definite and approachable by the discovery that the male germ is likewise a single cell, that fertilization of the egg is therefore the union of two cells, and that in con-

sequence the mechanism of inheritance must be stowed away somehow in these two cells.

Heredity in Unicellular Forms.—In unicellular animals one can readily see how it is possible for an individual always to give rise to its own kind. One of the simplest of the single-celled animals is the *Ameba* (Fig. 6, p. 28).

The ameba eats and grows as do other animals. Sooner or later it reaches a size beyond which it can not increase advantageously, yet it is continuously taking in new food material which stimulates it to further growth. Here then is a problem. The ameba solves this difficulty by dividing to form two amebæ. Such a division is illustrated in Fig. 6, p. 28. First the nucleus divides, then the cell-body. When the two new amebæ separate completely each renews the occupation of eating and growing. But what has become of the parent? Here, where once existed a large adult ameba are two young amebæ. The parent individual as such has disappeared, yet there has been no death, for we have simply two bits of living jelly in place of one. They will in turn repeat the same process, so will their offspring, and thus, barring accident, this growth and reproduction, or overgrowth as we may regard it, may, as far as we know, go on forever. Here the problem of heredity, or the resemblance of offspring to parent, is not a very complicated one. The substance of the cell-body and cell-nucleus divides into two similar halves, so that each descendant has the substance of the parent in its own body, though but half as much. It differs from the parent, not in quality or kind, but in size.

Reproduction and Heredity in Colonial Protozoa.—There are enormous numbers of these single-celled animals existing in all parts of the world. Some are simple like the ameba, others are very complex in structure. Many, after division, move apart and pursue wholly independent courses of existence. On the other hand we find a modification appearing in some which is of the greatest importance. After division instead of moving apart the two cells may remain side by side and further divide to form two more, these in turn may divide and thus the process goes on until there is formed what is known as a colony. Each cell of such a colony resembles the original ancestral cell because each is a part of the actual substance of that cell. As in the ameba, the first two cells are the ancestral cell done up in two separate packets, and thus finally the full quota of cells must be

so many separate packets of the same kind of material. Inasmuch as each is but a repetition of its original ancestor, it can, and at times does, produce a colony of the same kind as that ancestor produced.

Conjugation.—At longer or shorter intervals, however, we

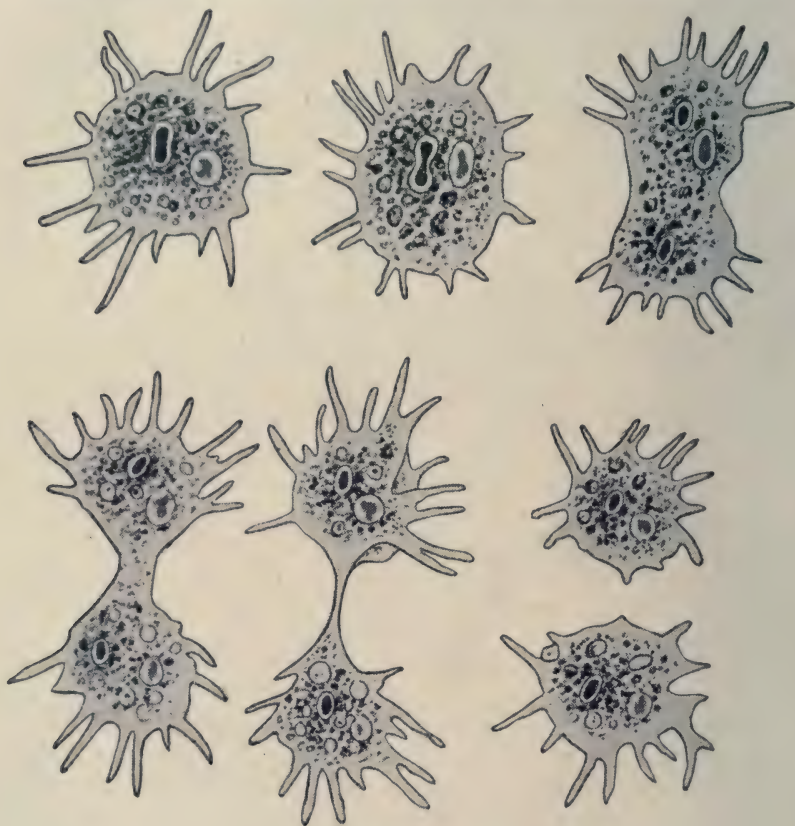


FIG. 6

Six successive stages in the division of *Ameba polypodia* (after Schulze). The nucleus is seen as a dark spot in the interior.

find that two individuals, on the disruption of the old colony, instead of continuing the routine of establishing new colonies through a series of cell divisions, very radically alter their behavior. They unite and fuse into a single larger individual.

This process is called *conjugation*. We find it occurring even in some species of ameba. The conjugating cells in some colonies are alike in size and appearance, in others different.

Specialization of Sex-Cells.—A beautiful sphere-shaped colony known as *Volvox* is to be found occasionally in roadside pools. Depending on the species of *Volvox* to which it belongs, the colony may be made up of from a few hundred to several thousand individuals arranged in a single layer about the fluid-filled center of the sphere and bound together by a clear jelly-like intercellular substance. Each individual cell also connects with its neighbors by means of thin threads of living matter. One of the largest species is *Volvox globator*, one edge of which is represented in Fig. 7, p. 30. Mutual pressure of the cells gives them a polygonal shape when viewed from the surface. Each cell, with a few exceptions to be noted immediately, bears two long flagella, whip-like structures which project out into the water. The lashing of these flagella gives the ball a rotary motion and thus it moves about. When the colony has reached its adult condition and is ready to reproduce itself, certain cells without flagella and somewhat larger than the ordinary cells become more rounded in outline and increase considerably in size through the acquisition of food materials. They are then known as egg cells or *ova*. Each ovum finally enters on a series of cell divisions forming a mass of smaller and smaller cells which gradually assumes the form of a hollow sphere like the parent colony. The young colonies thus formed drop into the interior of the parent colony and when this colony dies and disintegrates they escape later to the outside as independent swimming organisms.

The Fertilized Ovum Termed a Zygote.—After a number of generations of such asexual reproduction, sexual reproduction occurs. The ova arise as usual. Certain members of the colony, on the other hand, go to the other extreme and divide up into bundles of from sixty-four to one hundred twenty-eight minute slender cells, each provided with flagella for locomotion. When mature these small flagellate cells, now known as *spermatozoa*, escape into the interior of the parent colony and swim about actively. Ultimately each ovum is penetrated by a spermatozoon, the two cells fuse completely and thus form the single *fertilized ovum*, called also the *oöspERM* or *zygote*. The body-cells of the mother colony finally disintegrate. After a period of rest each

zygote, through a series of cell divisions, develops into an adult Volvox. In some species of Volvox a still further advance is seen, in that instead of both kinds of gametes being produced in the same colony, the ova may be produced by one colony and the spermatozoa by another. Here, then, we have the foreshadowings of two sexes as separate individuals, a phenomenon of universal occurrence among the highest forms of animal life.

Advancement Seen in the Volvox Colony.—In the Volvox colony there is a distinct advance over the conditions met with in various lower protozoan colonies in that only certain individ-

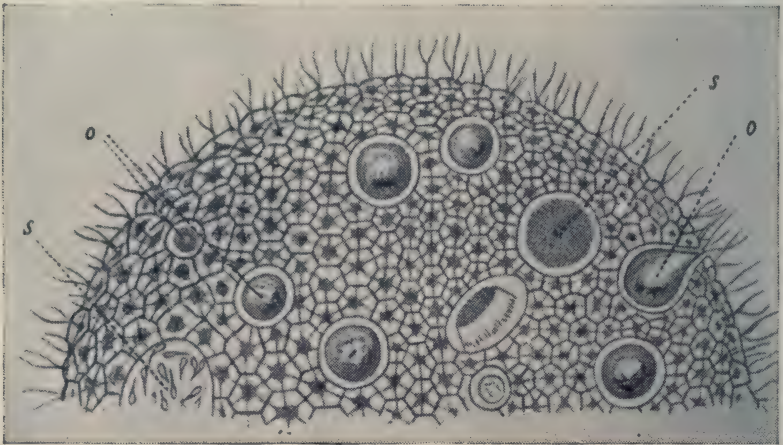


FIG. 7

Volvox globator (from Hegner after Oltmanns). Half of a sexually-reproducing colony: o, eggs; s, spermatozoa.

uals of the colony take part in the process of reproduction and these individuals are of two distinct types: one is a larger, food-laden cell or egg and the other a small, active, fertilizing cell. The motile forms are produced in much greater numbers than the eggs, plainly because they have to seek the egg and many will doubtless perish before this can be accomplished. This disparity in number is only a means of insuring fertilization of the egg. The remaining cells of the body carry on the ordinary activities of the colony such as locomotion and nutrition and have ceased to take any part in the production of new colonies.

Natural Death Appears with the Establishment of a Body

Distinct from the Germ.—Volvox is an organism of unusual interest because in it we see a prophecy of what is to come. Although still regarded as a colony of single-celled individuals, it represents in reality a transition between the whole group of unicellular animals termed protozoa and the many celled animals characterized by the possession of distinct tissues, known as *Metazoa*. Moreover, it shows an interesting stage in the establishment of a body, or *soma*, distinct from special reproductive cells which have taken on the function of reproducing the colony. In such colonial forms natural death is found appearing for the first time, the reproductive cells alone continuing to perpetuate the species. Then again Volvox represents an important step in the establishment of sex in the animal kingdom for in its sexual reproduction the conjugating cells known as *gametes* are no longer alike in appearance but have become differentiated into definite ova and spermatozoa.

In Volvox as in the other organisms which we have studied we find that all of the cells including the germ-cells are produced by the repeated division of a parent-cell, and consequently each must contain the characteristic living substance of that parent. Many other forms might be cited to illustrate reproduction in single-celled animals, whether free or in colonies, but all such cases would be practically but repetitions or modifications of those we have already examined.

Specialization in Higher Organisms.—If we pass on to the higher animals and plants which are not single cells or colonies of similar cells but organisms made up of many different kinds of cells, we find a pronounced extension of the phenomenon met with in Volvox. Instead of each cell executing independently all of the life relations, certain ones are set apart for the performance of certain functions to the exclusion of other functions which are carried on by other members of the aggregation. Thus the organism as a whole has all the life relations carried on, but, as it were, by specialists.

Sexual Phenomena in Higher Forms.—In the reproduction of multicellular organisms, one sees likewise but a continuation of the phenomena exhibited in Volvox. Ordinarily, each new form is produced by the successive divisions of a single germ-cell which in the vast majority of cases has conjugated with another germ-cell. In the development of the egg, as the divisions proceed, groups of cells become modified for their particular

work until the entire organism is completed. During development certain cells are set apart for reproduction of the form just as they were in *Volvox*. These two kinds of reproductive cells in multicellular organisms are derived ordinarily from two separate individuals known as male and female, though there are some exceptions. The main difference between these cells which will have to unite to form a single fertile germ-cell, is that they have specialized in different directions; one is small and active, the other large, food-laden and passive. But with two such germ-cells coming as they do from two individuals, one the male, the other the female, it is obvious that the actual living substance of which each germ is composed will be distinctive of its own parental line and that when the germs unite these distinctive factors commingle, hence the complications of double ancestry arise.

Structure of the Cell.—Before we can understand certain necessary details of the physical mechanism of inheritance we must inquire a little further into the finer structure of the cell and into the nature of cell division. A typical cell, as it would appear after treatment with various stains which bring out the different parts more distinctly, is shown in Fig. 5, p. 26. Typical, not that any particular kind of living cell resembles it very closely in appearance but because it shows in a diagrammatic way the essential parts of a cell. In the diagram, there are two well-marked regions; a central *nucleus* and a peripheral cell-body or *cytosome*. The substance of the cytosome is called *cytoplasm*. Other structures are pictured but only a few of them need command our attention at present. At one side of the nucleus one observes a small dot or granule surrounded by a denser area of cytoplasm. This body is called the *centrosome*. The nucleus in this instance is bounded by a well-marked nuclear membrane and within it are several substances. What appear to be threads of a faintly staining material, the *linin*, traverse it in every direction and form an apparent network. The part on which we wish particularly to rivet our attention is the densely-stained substance scattered along or embedded in the strands of this network in irregular granules and patches. This substance is called *chromatin*. It takes its name from the fact that it shows great affinity for certain stains and becomes intensely colored by them. This deeply colored portion of the cell, the chromatin, is of great importance from the standpoint of heredity. One

or more larger masses of chromatin or chromatin-like material, known as *chromatin nucleoli*, are often present, and not infrequently a small spheroidal body, differing in its staining reactions from the chromatin-nucleolus and sometimes called the *true nucleolus* or *plasmosome*, exists.

Cell Division.—In the simplest type of cell division the nucleus first constricts in the middle, and finally the two halves separate. This separation is followed by a similar constriction and final division of the entire cell-body, which results in the production of two new cells. This form of cell division is known as *simple* or *direct division*. Such a simple division, while found in higher animals, is less frequent and apparently much less significant than another type of division which involves profound changes and rearrangements of the nuclear contents. The latter is termed *mitosis* or *indirect cell division*. Fig. 8, p. 34, illustrates some of the stages which are passed through in indirect cell division. The centrosome which lies passively at the side of the nucleus in the typical cell (Fig. 8a, p. 34) awakens to activity, divides and the two components come to lie at the ends of a fibrous spindle. In the meantime, the interior of the nucleus is undergoing a transformation. The granules and patches of chromatin begin to flow together along the nuclear network and become more and more crowded until they take on the appearance of one or more long deeply-stained threads wound back and forth in a loose skein in the nucleus (Fig. 8b, p. 34). If we examine this thread closely, in some forms it may be seen to consist of a series of deeply-stained chromatin granules packed closely together intermingled with the substance of the original nuclear network.

As the preparations for division go on the coil in the nucleus breaks up into a number of segments which are designated as *chromosomes* (Fig. 8c, p. 34). The nuclear membrane disappears. The chromosomes and the spindle-fibers ultimately become related in such a way that the chromosomes come to lie at the equator of the spindle as shown in Fig. 8d, p. 34. Each chromosome splits lengthwise to form two daughter chromosomes which then diverge to pass to the poles of the spindle (Figs. 8e and f, p. 34). Thus each end of the spindle comes ultimately to be occupied by a set of chromosomes. Moreover each set is a duplicate of the other, because the substance of any individual chromosome in one group has its counterpart in the

other. In fact this whole complicated system of indirect division is regarded by most biologists as a mechanism for bringing about the precise halving of the chromosomes.

The chromosomes of each group at the poles finally fuse and two new nuclei, each similar to the original one, are constructed

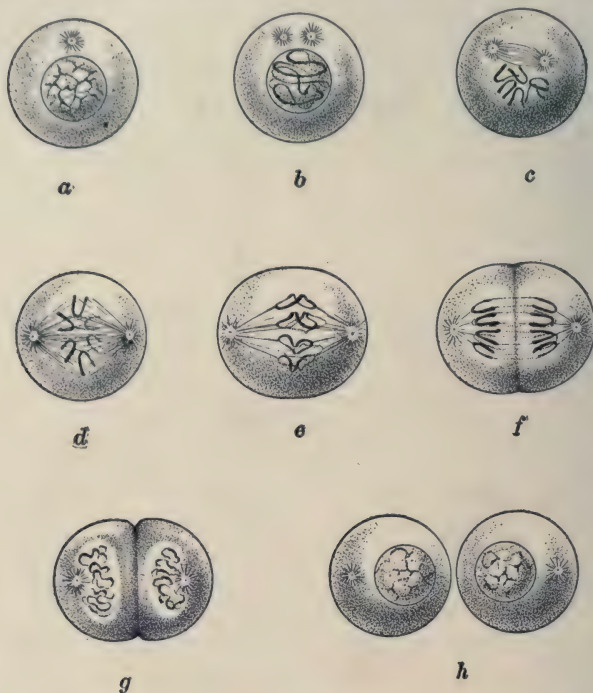


FIG. 8

Diagram showing representative stages in mitotic or indirect cell division: *a*, resting cell with reticular nucleus and single centrosome; *b*, the two new centrosomes formed by division of the old one are separating and the nucleus is in the spireme stage; *c*, the nuclear wall has disappeared, the spireme has broken up into six separate chromosomes, and the spindle is forming between the two centrosomes; *d*, equatorial plate stage in which the chromosomes occupy the equator of the spindle; *e*, *f*, each chromosome splits lengthwise and the daughter chromosomes thus formed approach their respective poles; *g*, reconstruction of the new nuclei and division of the cell-body; *h*, cell division completed.

(Figs. 8*g* and *h*, above). In the meantime a division of the cell-body is in progress which, when finished, results in the formation of two complete new cells.

As all living matter, if given suitable food, can convert it into living matter of its own kind, there is no difficulty in conceiving how the new cell or the chromatin material finally attains to the same bulk that was characteristic of the parent-cell. In the case of the chromatin, indeed, it seems that there is at times a precocious doubling of the ordinary amount of material before the actual division occurs.

Chromosomes Constant in Number and Appearance.—With some minor exceptions, to be noted later, which increase rather than detract from the significance of the facts, the chromosomes are always the same in number and appearance in all individuals of a given species of plants or animals. That is, every species has a fixed number which regularly recurs in all of its cell divisions. Thus the ordinary cells of the rat, when preparing to divide, each display thirty-eight chromosomes; many species of grasshopper, twenty-four; the lily, twenty-four; man, forty-eight; and the common house-fly only twelve. The chromosomes of different kinds of animals or plants may differ very much in appearance. They may be spherical, rod-like, filamentous or otherwise varied. In many organisms the chromosomes of the same nucleus may differ from one another in size, shape and proportions, but if such differences appear at one division they appear at others, thus showing that in such cases the differences are constant from one generation to the next.

Significance of the Chromosomes.—The question naturally arises as to what is the significance of the chromosomes. Why is the accurate adjustment which we have noted for their division necessary? The very existence of an elaborate mechanism so admirably adapted to their precise halving, predisposes one toward the belief that the chromosomes have an important function which necessitates the retention of their individuality and their equal division. Biologists accept this together with other evidence as indicative that in chromatin we have a substance which is not the same throughout, that different regions of the same chromosome have different physiological values.

When the cell prepares for division, the granules, as we have seen, arrange themselves serially into a definite number of strands which we have termed chromosomes. Judging from all available evidence, the granules are self-propagating units; that is, they can grow and reproduce themselves. So that what really happens in the splitting of the chromosomes is a precise halving

of the series of individual granules of which each chromosome is constituted, or in other words each granule has reproduced itself. Thus each of the two daughter cells presumably gets a sample of every kind of chromosomal particle, hence, the two cells are qualitatively alike. To use a homely illustration we may picture the individual chromosomes to ourselves as so many separate trains of freight cars, each car of which is loaded with different merchandise. Now, if every one of the trains could split along its entire length and the resulting halves each grow into a train similar to the original, so that instead of one there would exist two identical trains, we should have a phenomenon analogous to that of a dividing chromosome.

CHAPTER IV

EMBRYO FORMATION AND DEVELOPMENT

Early Theories.—The prevailing idea among most of the biologists of the seventeenth and eighteenth centuries was that one of the germs, either the egg or the male element, contained a completely formed but very minute organism—a perfect miniature of the adult. Development according to them was merely the expanding of the parts of such a germ. Bonnet (1720-1793) evolved his famous *preformation theory*, or *theory of encasement*, as the logical outcome of such a belief. He argued that inasmuch as an organism exists in a perfect though invisible form in the germ of the generation which precedes it, that germs in turn must include on a still smaller scale the complete germs of the third generation, and thus generation after generation, nested one within another like a series of juggler's boxes, the whole sequence of succeeding offspring are stored away. All germs were supposed to have been created at the beginning of the world. One enterprising exponent of the theory, indeed, computed that Mother Eve thus included over 200,000 millions of homunculi.

The researches of Wolff (1733-1794) and Von Baer (1792-1876), however, demonstrated conclusively that a young animal, such as the chick, is built up organ by organ, part by part, out of the egg and is not simply an unfolded and enlarged counterpart of the latter. We now know that the egg is a cell, with nucleus and cell-body, and that through repeated divisions of its own substance and the growth and specializations of the new cells thus formed, the body of the developing organism is built up.

Chief Processes Operative in Building the Body.—In the molding of the body and the building up of its special organs and tissues the chief processes operative are: (1) cell multiplication, usually accompanied by growth of the new cells; (2) infoldings and outfoldings of various cell complexes; (3) regional thickenings or thinnings; (4) special changes (*histological differentiation*) in groups of cells; (5) cell migrations or

rearrangements; (6) splittings and fusions of cell groups; and (7) occasionally resorption of certain areas or parts.

Cleavage of the Egg.—It is through a series of mitotic divisions, as described in the preceding chapter, that the zygote or fertilized egg-cell begins the construction of the new organism.

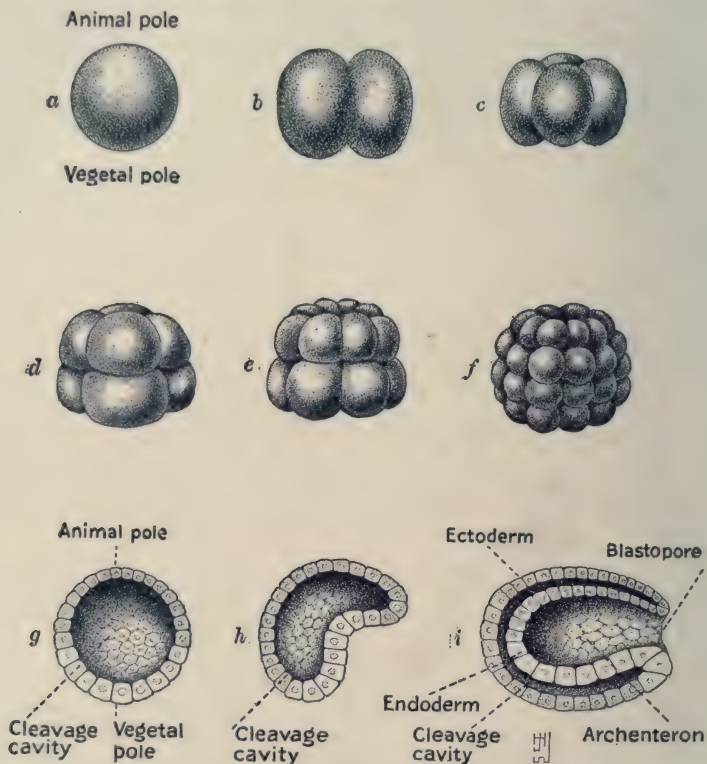


FIG. 9

Diagrams illustrating cleavage of the egg and formation of the two primitive germ-layers; *g*, *h*, *i*, are represented as cut in half. See text for description.

The process is technically spoken of as *cleavage*. Cleavage generally follows very shortly after fertilization. The fertile egg-cell divides into two, the resulting cells divide again and thus the process continues, with an ever-increasing number of cells.

These early cleavage cells (Fig. 9*b-f*, above) are known as

blastomeres. At first there is no appreciable increase in size of the total mass, the process being mainly one of parceling the original egg substance off into smaller and smaller cells. It is a noteworthy fact, however, since the nuclear material seems largely to govern development, that each blastomere, through the operation of mitosis, receives a full number of chromosomes, although individually each chromosome is smaller than its prototype in the uncleaved egg. The period of cleavage is tacitly regarded as ended when the successive divisions have reduced the cell size to a physiological minimum and the organism begins to grow and establish specialized parts.

As a matter of fact in very many eggs there is so great an accumulation of yolk as markedly to modify cleavage and the subsequent processes leading to embryo formation, but inasmuch as, no matter how devious the route, the ultimate outcome is essentially the same in all—namely, the formation of the so-called *germ-layers* out of which the various *tissues* and *organs* of the individual are shaped—we may for purposes of exposition select a more or less hypothetical case, which will show in a diagrammatic way the nature of the changes undergone in a developing vertebrate. It should be borne in mind that this has been done in the following account which is merely a sketch of the underlying plan upon which the development of vertebrates is based.

The Blastula.—As cleavage proceeds, subdividing the original egg-cell into a many-celled embryo, the cells of this embryo become arranged into a single-layered spherical mass, termed a *blastula*, inclosing a central cavity known as the *cleavage* or *segmentation cavity*. Fig. 9g represents such a blastula cut in half. In the egg a chief axis is usually recognizable so that we may speak of the ends of this axis as the *poles* of the egg. These are designated as the *animal* and the *vegetal* poles respectively. In nearly all eggs there is at least a trace of yolk and these poles may be often identified through the tendency of the yolk to accumulate toward the vegetal pole while the nucleus is displaced to some extent toward the animal pole. This same polarity is observed in the blastula, that part corresponding to the animal pole of the egg being still termed the animal pole, and likewise for the vegetal pole.

The Gastrula; Ectoderm and Endoderm.—The blastular stage is followed by one which is essentially a double-layered cup, having much the appearance produced by denting in the

side of a hollow rubber ball. In the developing vertebrate, however, the process is not so simple as the mere invagination of one side of a hollow sphere; it is only partially of this nature. At a point about midway between the animal and vegetal poles, on what may be called the posterior dorsal side of the blastula, certain cells become extremely active in division and this region of activity gradually extends sidewise around the blastula. At the same time the cells at the vegetal pole flatten and begin more or less passively to swing inward (Fig. 9*h*, p. 38). Thus the two-layered condition is produced by a combined process of actual folding-in of the vegetal hemisphere and the ingrowth of a layer of cells formed as a result of the active cell proliferation just mentioned. The segmentation cavity is thus partially obliterated and the developing organism now known as the *gastrula* (Fig. 9*i*, p. 38), has a new cavity which is called the *archenteron* or primitive gut. The outer of the two layers is termed the *ectoderm*, the inner, the *endoderm*. The opening through which the archenteron communicates with the exterior is the *blastopore*. That part of the endoderm formed by the ingrowth of the new layer of cells is the roof or dorsal wall of the archenteron, the part formed by invagination is the floor or ventral wall.

Changes in the Gastrula.—The gastrula gradually elongates, largely through a rapid cell multiplication in the zone where ectoderm and endoderm unite at the blastoporal opening, so that the blastopore itself is displaced toward the rear. In this process of displacement it assumes, in many vertebrates, the outline of an elongated slit which fuses in front, and as the elongation continues, the process of fusion creeps backward, ultimately completely sealing together the two lips of the blastopore. Thus, in such forms, after the embryo has attained this elongated form, a scar-like streak, known as the *primitive streak* (Fig. 11, p. 45) may be seen along the mid-line of the back. In a few simple forms the hindermost part of the blastopore never closes completely but persists in part as the vent of the alimentary canal. The vent or anus, in the majority of vertebrates, however, is of different origin to be noted presently.

Fig. 10*a*, p. 44, represents in highly schematic form a section cut transversely from an embryo in the two-layered condition. The upper or dorsal flattening of the ectoderm indicates the first appearance of the nervous system.

Formation of the Mesoderm.—A number of simultaneous changes now occur; among other things a third germinal layer (really a double layer), the *mesoderm*, makes its appearance. From both the region of the primitive streak and in front of it, the mesoderm grows out on each side pushing its way between the ectoderm and the endoderm. In front it arises, in some simple forms at least, as a distinct double fold or outpocketing of the archenteron (Fig. 10*b*, p. 44). In such cases it has its own cavity from the first. In most vertebrates, however, the mesoderm arises as a solid outgrowth which later splits to form a cavity. In any event, it comes to contain a cleft or cavity which separates it into an outer and an inner layer. This cavity later gives rise to the *body-cavity* or *cœlom*. Soon the newly formed mesodermic pouches pinch off completely from the endoderm (Fig. 10*c*, p. 44). Posteriorly, however, as the embryo elongates rapidly by multiplication and growth of cells in the blastoporal region, a general, thick, undifferentiated mass of cells is produced. This mass soon splits up into definite layers, which become continuous respectively with the original ectoderm, endoderm and mesoderm. The cœlomic spaces of this posterior mesoderm arise as clefts by the rearrangement of the mesodermal cells which themselves are not definite outgrowths from the archenteron, as they were further forward.

The mesodermal pouches develop and extend rapidly (Fig. 10*d*, p. 44), gradually spreading downward to meet in the mid-ventral line. The outermost wall of each mesodermic sac spreads along and fuses with the ectoderm, the inner one becomes closely applied to the endoderm.

Stages in Embryo Development.—Thus the embryo has come to consist essentially of two tubes, the outer one forming the body-wall, the inner one the alimentary tract (Fig. 10*e*, p. 44). This general arrangement is a sort of archetype for all higher animals.

Meanwhile other important changes have been in progress in the embryo. The mid-roof region of the archenteron has become thickened and rolled into a rod extending the length of the body (Figs. 10*b*, *c*, *d*, p. 44). It becomes pinched off entirely from the endoderm and is known as the *notochord*. This is a skeletal rod around which the vertebral column is built.

Coincident with the foregoing changes the dorsal region of the ectoderm has been rapidly altering. Along the mid-line a

strip of ectoderm sinks down, its margins become more or less elevated to form folds which eventually roll together and fuse to form a tube which becomes the brain and spinal cord (Figs. 10*b, c, d*, p. 44). The brain region arises with much wider folds than the spinal cord region and this larger size persists when the tubular condition is attained. Ultimately the remaining ectoderm meets above this *neural tube* and fuses so that the latter lies beneath the outer surface of the body. The central nervous system never completely loses its hollow condition; the spaces in the brain region become the *ventricles* and other cavities of the brain; and the cavity of the cord persists as the small *neural canal* of the adult spinal cord (Fig. 10*f*, p. 44). The brain is at first marked off into three *primary brain vesicles* from which the complicated parts of the adult brain are built up.

It should be noted that in the meantime the mesodermal tissues besides spreading downward to meet in the mid-ventral line have also extended upward along either side of the notochord and the central nervous system. This upper region of each mesodermal pouch soon becomes marked off lengthwise of the embryo by a series of constrictions into a row of cubical segments termed *mesodermic somites* which will give rise to the skeletal tissue and the main musculature of the trunk (Figs. 10*d, e*, p. 44). Ultimately a longitudinal constriction (Fig. 10*e*) completely cuts off this series of hollow blocks, and a segmented zone immediately beneath them, from the main cavity below, which persists as the body cavity proper of the adult.

From the middle segmented zone just mentioned, beneath the muscle segments, part of the primitive excretory or *nephridial system* (Fig. 10*e*) arises but its origin is too complicated to be discussed in an elementary review of development. From the inner wall of the middle zone a number of cells rapidly bud off. Some migrate inward, gradually surrounding the notochord and central nervous system (Fig. 10*e*), where they will eventually give rise to the *vertebræ* of the spinal column. Others wander downward between the endoderm and its investing layer of mesoderm where they supplement the latter in forming the smooth muscles and connective tissue of the alimentary tract. Some come to form partitions of connective tissue between the muscle segments and still others pass outward and give rise in part to the deeper layers of the skin.

The mesodermal layers bounding the body-cavity proper give

rise to the flattened layer of cells (*peritoneum*) which lines the body-cavity on the one hand and encases the alimentary canal and its outgrowths on the other. Above and below the digestive tract the layers press inward toward the mid-line to form a double-layered partition (Fig. 10e) between the right and left halves of the body-cavity. They thus form the membranous *mesenteries* by which the various viscera are held in place. The lower (ventral) mesentery, never complete, breaks away more and more in the posterior part of its course so that in the abdominal region of the animal the two halves of the body-cavity communicate freely below.

The original gastrular mouth (*blastopore*), as indicated in Fig. 9i, p. 38, does not remain in most vertebrates as a permanent structure. At one stage in the formation of the nervous system the *neural folds* roll together in such a way as to effect a transitory connection between the canal of the neural tube (Fig. 10f, p. 44), and that of the alimentary tract by way of the blastopore, but this connecting canal (*neurenteric canal*) soon disappears leaving the alimentary tract a closed tube without either mouth or vent. The latter are formed by inpushings of the ectoderm from without. Pit-like orifices appear (Fig. 10f), which dip in to come in contact with the endoderm. Eventually they break through at the points of contact and so complete the canal. Thus the beginning and the termination of the alimentary tract are lined by ectoderm and the remainder of it by endoderm.

The digestive system of the adult is built up by changes in this simple tube, brought about mainly through local enlargements, growth in length which involves coiling, and various foldings and pocket formations. The liver first appears as a single tubular evagination from the digestive tube, later becoming branched. Other glands for the elaboration of various digestive juices form in the walls of the tract itself through processes of infolding and outfolding together with the specialization of their component cells. The lungs originate as a single median outgrowth which soon bifurcates into two pouches (Fig. 12A, p. 48).

Organs Derived from the Different Germ-Layers.—At this point it may be well to enumerate in a general way what portions of the adult animal are ordinarily derived from each germ-layer, bearing in mind, however, that most embryologists of to-day look on such a classification by germ-layers as a matter of convenience rather than one of great significance.

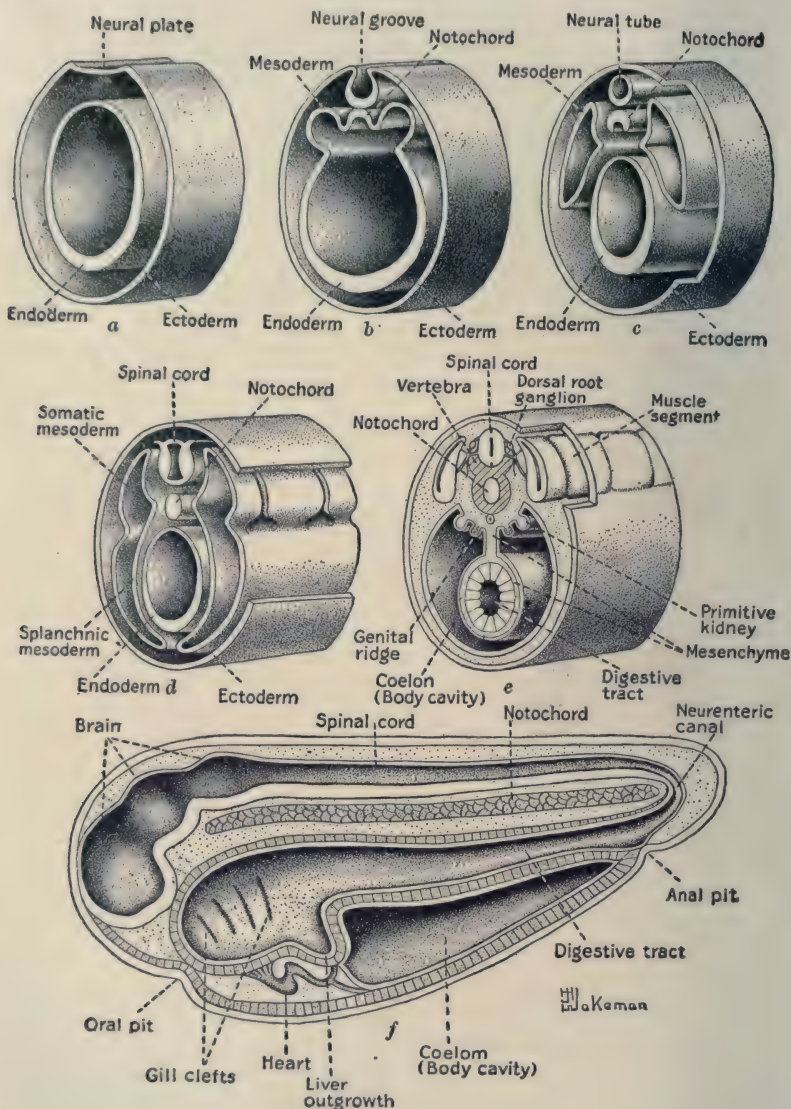


FIG. 10

Diagrams representing stages in the development of a vertebrate: *f* represents the embryo cut in half to show inside view. See text for description.

From the *ectoderm* arise the outer portion (*epidermis*) of the skin together with the functional cells of its glands; the essential parts of the nervous system and the sensory portions of all sense organs; the lining of the nose, mouth, and vent; the enamel of the teeth; the lens of the eye; and the nails and hair.

The *endoderm* gives rise to the wall of cells lining the digestive tract (except its beginning and termination) together with the various outgrowths such as the larynx, trachea, thymus and thyroid glands, lungs, liver and pancreas, associated with it; likewise, the lining of the bladder and, in part, of the outlet (urethra) from it.

From the *mesoderm* are formed the lining of the body-cavity and other serous cavities; the deeper layer of the skin, the kidneys and most of the reproductive system; the muscles; the various supporting and connective tissues (with a few exceptions), including bone and the dentine of the teeth; the muscular and outer covering of the digestive tract and its outgrowths; and the vascular system including heart, blood, blood-vessels, and lymphatics.

Yolk as a Modifying Factor in Cleavage and Embryogeny.—Yolk is a food material which accumulates in eggs usually in the form of granules or platelets and is for the nutrition of the developing embryo. It varies greatly in relative amount in the eggs of different kinds of animals and is one of the chief factors in determining differences of size in eggs. The size of an animal has nothing to do with the size of the egg: for example, the egg of a rabbit is only one-sixteenth the size of a frog's egg.

The amount of yolk present largely determines, in egg-laying forms, the developmental condition of the young at hatching. If there was little yolk originally, then the young will have to begin to shift for themselves early. More yolk usually means a farther lift along the road of development. In reptiles and birds are found unusually large eggs and, furthermore, the yolk proper is supplemented by additional nutrition in the form of the so-called "white." It should be borne in mind, that the real egg

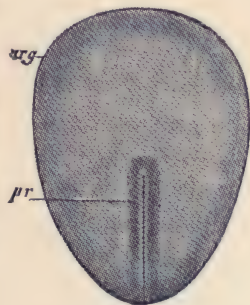


FIG. II

Embryonic area of a rabbit showing primitive streak, *pr*. (From Bal-four after K  lliker.)

of such forms is the "yellow," an enormously distended cell in which the yolk has accumulated to such an extent as to crowd the nucleus and much of the cytoplasm over to one side where, in the hen's egg for instance, they may be identified as a small scar-like disk.

The Egg of Most Mammals Small Because of Other Means of Nourishment.—Among the mammals, however, with the exception of a few primitive egg-laying forms, the eggs are small. Thus the human ovum measures only about 0.2 mm. ($1/27$ inch) in diameter. But in such mammals, a means has arisen for directly absorbing nourishment from the mother and has thus done away with the necessity of much yolk in the egg. The young are retained within the body of the mother, in what is known as the womb or *uterus*, until well along the path of development, and even after birth they are further provided for some time with food in the form of milk elaborated in the mammary glands. Notwithstanding the fact that there is little yolk present in the ova of the higher mammals, we find that certain peculiar, round-about methods in the development of the mammalian ovum are explicable only on the supposition that it was once heavily yolk-laden and that some of the accompanying adjustments to this condition have been handed down through inheritance.

Human Embryo and Fetus.—In man the developing child is commonly called the *embryo* until about the end of the second month, after which it is termed the fetus. There is no sharp line of division between embryo and fetus. The criterion is the establishment of the primary parts or organs of the body such as limbs, brain, eyes and viscera. Since these are formed gradually and some arise earlier than others, any terms based on their time of appearance must obviously be elastic. Practically all of the fundamental organs of the body are established and well started in development by the end of the second month. Fig. 13, p. 52, shows the external appearance of the human embryo at the ends of about the *first* and *second months* of development, respectively.

At the end of the *third month* the human fetus weighs only about $\frac{3}{4}$ of an ounce and is approximately 3 inches long. By the end of the *fourth month* it weighs between 4 and 5 ounces and measures about 6 inches in length; the muscles of the limbs are capable of producing movements; ossification is beginning in certain bones of the skull; sex is recognizable. The end of

the *fifth month* finds the fetus weighing some 10 ounces and measuring 10 inches in length; hair and nails appear; ossification in the pelvic bones (*ischium*) is in progress.

By the end of the *sixth month* a weight of 1 pound and a length of 11 to 12 inches has been attained; closed eyelids with eyelashes are discernible; and fat is developing under the skin. At the conclusion of the *seventh month* the fetus usually weighs some 3 or 4 pounds and is from 13 to 15 inches long; the eyelids are open; considerable fat is present under the skin and the skin is covered with a greasy (sebaceous) substance. By the end of the *eighth month*, the weight is about 4 or 5 pounds and the length, from 16 to 18 inches; the nails are completely developed. At the end of the *ninth month*, which is known as *full term*, the fetus, now ready for birth, weighs from 5 to 9 pounds (the general average is about $6\frac{1}{2}$ pounds) and has a length of from 17 to 21 inches. In general at birth the male infant exceeds the female by about 12 ounces in weight. A child weighing less than 5 pounds at birth rarely thrives, though a few cases are on record of children surviving who, when born, weighed only 1 pound.

Not All Structures Permanent.—Curiously enough in all vertebrates, including man, in the region of the pharynx, pairs of lateral *pharyngeal pouches* (gill clefts) grow outward toward the surface (Fig. 10f, p. 44) where they meet corresponding inpocketings from the ectoderm (Fig. 12B, p. 48). In this way primitive gill clefts and gill arches are formed. Moreover the main arterial blood-vessel (*ventral aorta*) from the two-chambered heart (one auricle and one ventricle) sends branches into each arch just as if the arches were going to bear functional gills. In lower vertebrates such as the fishes and amphibia these clefts break through and form definite slits which become functional gill slits, but in all higher vertebrates they are only transitory structures which disappear or become remodeled into other structures. The only normally persisting part of the clefts in higher animals (including man) is part of the first which becomes the *middle ear* and the *Eustachian tube* which connects it with the pharynx. In rare cases of abnormal development another cleft may break through and persist as a slit in the throat region technically known as *cervical fistula*.

Vestigeal Structures.—Such a formation of gill arches and gill clefts by animals which will never require the use of func-

tional gills is only one of the numerous instances that might be cited of transient structures which appear in the course of development but which later become mere rudiments or are molded into different organs characteristic of a higher type of animal. Biologists look on such evanescent structures as reminiscent of the past ancestry of the form in question. They are believed to have at one time formed the basis of functional organs but in the course of long ages, with gradual changes in the structure and mode of life of their possessors, their original functions have lapsed, though they have lingered on, in part like the silent letters of certain words, and in part as the foundations upon which newer organs have been built.

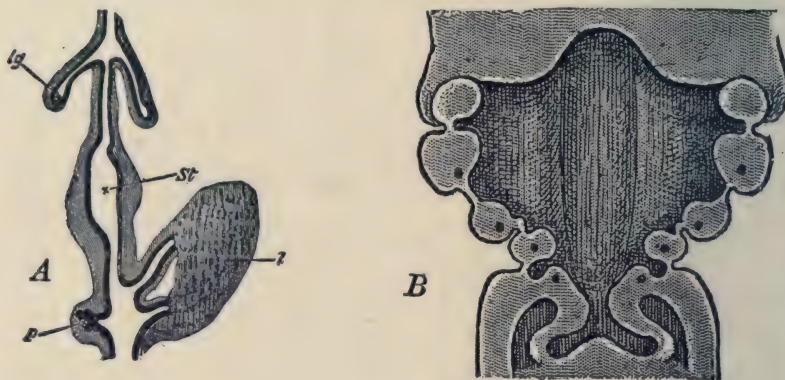


FIG. 12

A. Diagram of a portion of the digestive tract of a chick after four days of incubation (from Balfour after Götta). The black inner line represents endoderm, the outer shading the mesoderm; *lg*, outgrowth which will form one lung; *st*, stomach; *p*, pancreas; *l*, liver.

B. Diagram showing mouth and throat cavity of a very young human embryo in longitudinal section (after Hertwig from His). The rounded gill arches on either side are cut across, some showing the cut ends of the main arch blood-vessels. The outpocketing of the endoderm and the inpocketing of the ectoderm forming the clefts are seen between the arches.

Explanations of Certain Congenital Defects in Man.—Various congenital defects in man are retentions or extensions of conditions or structures that are of perfectly normal occurrence in the earlier stages of embryo formation. Two of the commonest of these are perhaps *harelip* and *cleft palate*. In the fetus the upper lip is formed by the fusion of two lateral parts

with a central part, across two deep, wide grooves which connect the early mouth with what will become the nostrils. If these parts fail to unite the result is a harelip; that is, a cleft or groove is left between each nostril and the mouth. If the fusion fails to occur on only one side then the more usual single harelipped condition is produced.

Cleft palate is not infrequently combined with harelip. It too is the result of an arrest of development in which two early embryonic halves are prevented in some way from fusing as they should normally do; thus, an earlier embryonic condition persists into the adult. The suppression, however, is one which occurs at a later stage of development than that productive of harelip, for while in the normal human embryo the parts of the upper lip are united before the end of the second month, the fusion of the right and left halves of the palate to form the roof of the mouth is not completed before the end of the third month. A complete palate occurs only in mammals. Its obvious use is to enable the young to suckle and swallow without regurgitating food through the nose. Since it separates the nasal passages from the mouth it also permits an animal to breathe freely while masticating food. A child with a cleft palate is, as far as this structure is concerned, in much the same condition anatomically as that which is the normal state in amphibians and reptiles. A tendency toward the formation of harelip and cleft palate apparently runs in certain family strains.

Various deviations from normality may occur in the viscera. For instance, surgeons have found men who have been born with their abdominal organs arranged and attached as if the individual were going to walk on all fours. While this stage of development occurs normally in the earlier stages of human embryology it should later shift so that the visceral organs may become more closely bound down to fit them for the upright condition of man.

Occasionally individuals are met with in whom the viscera are transposed. The arch of the aorta bends to the right instead of the left, the apex of the heart is directed toward the right so that its beat is felt on the right side, the large end of the stomach is toward the right and the cæcum and appendix toward the left—in short all of the viscera are reversed in the same symmetrical way that the left hand is a reversed pattern of the right. No satisfactory explanation has ever been given, embryo-

logically or otherwise, to account for such a transposition of the internal organs.

In lower vertebrates, birds, and the simplest mammals, the alimentary tract and the genital and urinary ducts all open into a common terminal chamber known as the *cloaca*. This same condition prevails in the embryos of higher mammals including man but subsequently the uro-genital passage becomes separate from the opening of the alimentary tract. Occasionally, however, a child is born in which the cloaca persists in its primitive form.

In some instances a child is born in which the partition formed between the alimentary tract and the invagination from the exterior (Fig. 10f, p. 44) to form the vent fails to break through thus leaving no terminal outlet to the bowel.

Again, various congenital heart malformations can readily be traced to failure of the parts concerned to pass on properly from some stage of development which is in itself perfectly normal. For example, in gill-breathing animals, such as fish, the heart is a single pump with one auricle and one ventricle which has to drive the blood through the gills to the rest of the body. In higher animals, as mammals, the heart, however, is a double pump with two auricles and two ventricles running two distinct circuits, one to the lungs, and the other to the body. As already indicated, the higher vertebrates in embryo all have at first this simpler type of circulation, a tubular heart with one auricle and one ventricle which sends blood forward to the gill arches. In these higher forms, however, when the gill arches begin to disappear or transform into other structures and the lungs commence to develop, a readjustment of the circulatory system occurs. The heart twists into more or less of an S-shaped structure and certain fusions and modifications come about. At one stage there is one common ventricle and two auricles—a condition which is the permanent one in some fishes, in amphibia and in most reptiles—but in birds and mammals a partition forms which divides the original ventricular chamber into distinct right and left ventricles. However, as a malformation in man, cases are found in which the partition fails to form completely.

A commoner heart malformation in the child is one in which an opening (*foramen ovale*) in the partition *between the auricles* fails to close as it should shortly after birth. In the fetus, since the lungs are not functioning for respiration, most of the oxygenated blood which returns to the heart from the placenta is shunted

directly across from the right auricle to the left auricle and thence through the left ventricle to the body. The moment that the placental circulation is cut off the child must begin to breathe. When the lungs expand the course of the blood is shifted so that a complete pulmonary circulation is established. Thereafter the right auricle receives only venous blood and the left auricle, only arterial (oxygenated) blood. In some 25 to 30 per cent. of individuals the closure of the foramen in the septum between the auricles is incomplete, but inasmuch as the edges overlap, they are pressed so firmly together by the blood on the two sides when the auricles contract that there is no intermingling of venous and arterial blood. Occasionally, because of imperfect or inhibited growth in the septum, the foramen remains sufficiently open to permit of such an intermingling. This causes a dark color in the skin, producing what is commonly known as a "blue baby."

Of various suppressions in connection with the nervous system may be mentioned cases of brain arrest found in small-headed or microcephalic idiots. In extreme cases the brain may be but slightly heavier than that of one of the higher apes and the fissures and convolutions distinctly simian-like in their simplicity. As rare monstrosities, cases are on record in which the top of the head is absent from lack of brain development, or those in which the spinal cord remains exposed as a flat plate along the back having never become tubular and submerged below the surface as occurs in normal development.

Still another anomaly that may occur in man which probably harks back to the persistence of an earlier embryonic state is the existence of additional breasts or nipples. In the embryo of some mammals such as the pig, a *mammary* or *milk ridge* extends along each side of the body from armpits to groins. The same condition has been found to occur in some early human embryos. In such forms as the sow or cat, *mammæ* are formed at intervals along the entire length of these ridges. Supposedly this was the arrangement in primitive ancestral mammals. As abnormalities in men and women additional *mammæ* or nipples may be formed above or below the usual pair of breasts. Such a condition is commonly regarded as a reversion to the ancestral type.

While a considerable number of other anomalies due primarily to abnormal retention, sometimes coupled with exaggeration, of early embryonic structures might be cited, our account will have

to close with but one more example, the well authenticated though rare cases on record of children who have been born with true tails. In the human embryo of the third or fourth week of development (Fig. 13*A*, below) a well-defined tail is a perfectly normal structure although it later becomes submerged by the growth of adjoining parts. In human dissections, it is not uncommon to find vestigial muscles passing to the coccyx which correspond to the tail muscles of lower animals. So that a child born with a tail has merely retained and overdeveloped, as

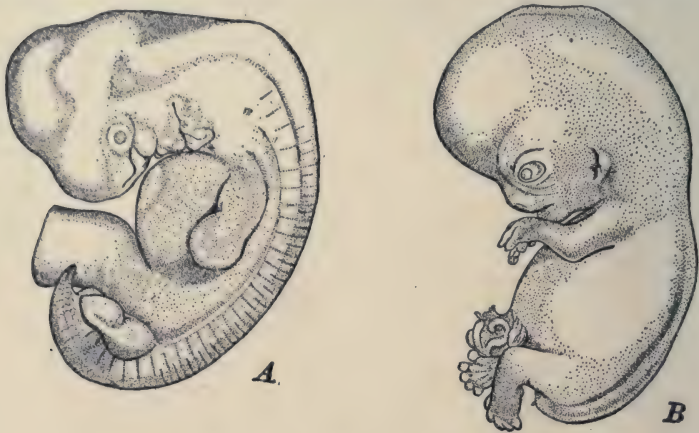


FIG. 13

A, human embryo of about four weeks; *B*, human embryo of about two months; *B* is drawn on a smaller scale than *A*. (From Conklin after Keibel.)

an abnormal structure, what is perfectly normal in its early period of embryogeny.

The Fetal Membranes.—The embryos of all vertebrates above the fishes and amphibians are provided with rather elaborate auxilliary structures known as the *fetal membranes*. These surround the developing individual, protecting it and keeping it under suitable conditions of nutrition, moisture and respiration. All mammals except a few primitive forms have evolved a system of obtaining nourishment directly from the mother, through an elaboration of the fetal membranes. Branching processes are sent out which come to fit into corresponding pits in the uterine wall of the mother. The structure thus formed, called a *placenta*, is the essential organ of nutrition, excretion and respiration of

the embryo in the higher mammals. There is much variety in its complexity and arrangement in different kinds of mammals but the function is the same in all. In man, the higher apes, bats, insectivores and rodents, the placenta is of a *discoidal* type, so named because the branching processes (*villi*) are grouped together in one large disk.

The development of the human fetal membranes and placenta is complex and difficult to understand, but inasmuch as these structures are the culmination of a long series of specializations, various stages of which are still in evidence in other mammals, the structural correspondence may be traced through comparative study of these simpler forms. Such a review, however, is beyond our present scope.

Fig. 14, p. 54, is a diagrammatic representation of the human embryo at an early stage of its development in the uterus, with some of the more important parts named. The embryo becomes surrounded by two distinct membranes. The one nearer it is called the *amnion*, the other one, the *chorion*. The space between the embryo and the amnion becomes filled with a watery fluid which protects the embryo from mechanical shocks.

As the young embryo shapes up it closes in along the ventral surface until only a small orifice connects the body-cavity with its extra embryonic extension inclosed by the fetal membranes. This constitutes the *umbilicus*. From the umbilical region, as the fetal membranes take final form and the embryo develops, the edges of the umbilicus grow out ventrally, forming a tube that finally comes to make up a cylindrical cord (*umbilical cord*) which extends from the ventral surface of the embryo's body to the placental portion of the chorion, thus suspending the fetus in a fluid-filled cavity. The navel of the born individual is the depression or scar on the abdomen where the umbilical cord of the fetus was attached.

No Direct Blood Circulation nor Nervous Connection between Mother and Child.—While the interpenetration of the embryonic and maternal parts of the placenta are very intimate in such forms of placentation as that of man, and although interchange of gaseous and other dissolved substances take place between fetal and maternal blood, it should be borne in mind, nevertheless, that there is no direct connection between the two sets of blood-vessels, and therefore no actual circulation of the mother's blood through the blood-vessels of the fetus. A cross-section of the umbilical cord shows the cut ends of two *umbilical*

arteries and a single *umbilical vein* imbedded in a mass of connective tissue; there are no nerves, hence, the only path of communication between mother and fetus is the indirect one by way of the blood stream. This is an important consideration to keep in mind when one meets with the cherished folklore of transmitted mental impressions of the mother which are popularly supposed to bring about all sorts of changes in the fetus.

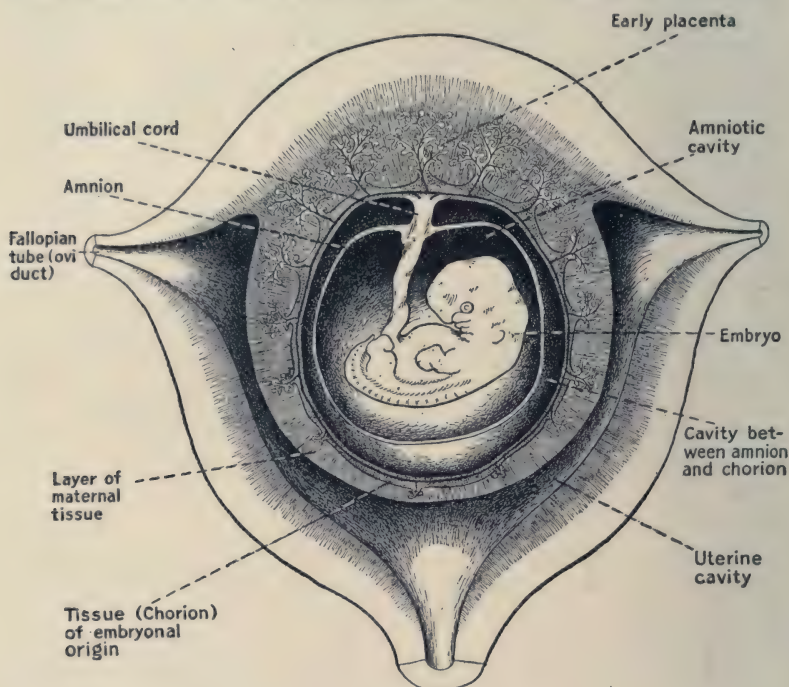


FIG. 14

Schematic illustration to show very young human embryo in the uterus, and the relation between them.

The mere attempt to answer the question *how*, when one understands the real physical relation between mother and fetus, shows the utter improbability of such transmission.

Usually the amnion ruptures before the delivery of the child and is later expelled as part of the *afterbirth*, but occasionally it remains unbroken and the child is born with a "caul" or "veil." The popular superstitions about the good luck of such individuals or their powers of looking into the future are wide-spread.

CHAPTER V

THE MECHANICS OF DEVELOPMENT

How Much is Preformed in the Egg?—How much the newly developed creature is a result of specific, preformed substances in the egg and how much it is the outcome of influences imposed from without has been a bone of contention ever since the beginning of embryological study. It is obvious at least that inasmuch as the new being is built up through a series of cell divisions, its various parts could not have been contained in the egg in miniature in the crude way the early preformationists believed; and it is equally evident that the germ can not be a simple, unorganized mass.

The problem is an extremely complex one. On many points we are yet in the dark. That there are special determining factors present in the germ is certainly evidenced by the fact that we may take two eggs which look alike and put them into an aquarium of sea water so that they will develop under the same conditions yet one will produce a back-boned animal and the other an invertebrate. The egg of a bird can never give rise to a frog no matter what external conditions prevail, because the egg of the bird is not of the same organic constitution as the frog's egg to begin with. That the potentia of the characteristics of the adult are in some way existent in the germ can not be gainsaid; but in what form? How are they released or expressed?

Normal development implies an appropriate environment, and, as a matter of fact, the natural environment under which the development of any kind of organism comes about is a fairly constant combination of external factors. But what would happen if we radically altered this environment in some one or more particulars? Can we bring about effects not normally occurring in nature? If alterations can be produced, this should give us a means of prying into the mechanism of development and obtaining some side-lights on the methods of hereditary expression. Embryologists have realized these possibilities and in the past few years have done much work to test out various aspects of the problem.

Fundamental Factors in Development.—Broadly speaking four factors of fundamental importance are involved in development. These are: (1) The nature of the primitive stuffs of which the germ is composed; (2) The influence of the external conditions which we call environment; (3) The chemical, mechanical or other influences exerted by some parts of the developing body on others; and (4) The stage of development at which a stimulus acts.

The third factor is reducible to special phases of the others but inasmuch as there are indications that the normal growth of each tissue or organ is probably controlled by one or more specific internal secretions from other tissues or organs—producing their effect, in part at least, by inhibiting or accelerating the development of the given part—it is perhaps well for purposes of description to regard such influences as a distinct set of factors.

Slight variations in external conditions are constantly occurring and since they produce no appreciable effect on the developing form, they are to be regarded as part of the normal environment. It has been found, however, that pronounced alterations of such extrinsic factors as temperature, pressure, gravity, light, moisture or chemical constitution of the surrounding medium may affect development either generally or specifically, not infrequently producing monstrosities. On the other hand, a very slight alteration of the internal conditions will in all probability produce a marked effect.

Separation of Early Cleavage Cells.—The results of interference with normal conditions of environment can easily be demonstrated by actual examples. Sea water lacking one of the three elements, sodium, calcium, or potassium, tends to make the early cleavage cells of the eggs of various marine organisms fall apart; certain acids do the same; and the result may also be accomplished by shaking and by other mechanical means. Such isolated cells, or *blastomeres*, if placed in normal sea water may continue to develop. It has been found that, as extremes, there are two types of behavior. In the one type each blastomere gives rise to a complete new organism, in the other only to a part of one. Thus in the first case if the first two blastomeres are separated each will develop independently and twins will be formed. On the other hand, if the behavior is of the second type each blastomere although continuing to develop will, as the case may be, form approximately only the right or the left half of an individual.

Determinate and Indeterminate Cleavage.—In the development of *Amphioxus*, a small primitive vertebrate-like form, for example, the early blastomeres, if separated, will each give rise to a normal, though proportionately smaller, embryo (Fig. 15*B*, below). That is, what is destined normally to produce one individual can be made to give rise to two or even more. In some jelly-fish each cell of the sixteen-cell stage may thus be made

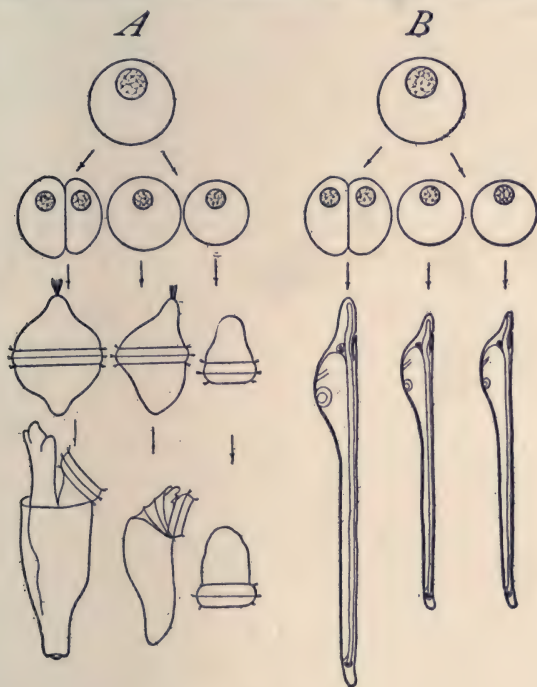


FIG. 15

Diagram illustrating development of entire eggs and of isolated blastomeres of two-celled stage (after Wilson). *A*, *Dentalium*: at the left, development of the whole egg; at the right, development of the isolated first two cells, producing two defective larvæ. *B*, *Amphioxus*: the corresponding experiment; isolated cells producing two perfect dwarfs.

to develop into a perfect, though dwarfed, embryo. In such cases, at least, the blastomeres are equivalent in their potentialities during early cleavage. On the other hand in such a form as *Dentalium*, a mollusk, the first cleavage plane marks out the developing individual into right and left halves so that when

the two blastomeres are separated, each develops into only a half or partial embryo (Fig. 15*A*, p. 57). We speak of the two different conditions as the result of *indeterminate* and *determinate* cleavage respectively. In the indeterminate form all blastomeres up to a certain point of development are of equal value among themselves, and they differ from the original ovum, not as regards specific or related parts, but only in amount of substance; so that any one of them can give rise to a new individual. In the determinate form, on the contrary, specialized egg substances outside the nucleus exist apparently from the first and seem to be so arranged that the first cleavage plane cuts off materials in one blastomere that are not present in the other. As a matter of fact, the two types of cleavage are not absolutely distinct from one another because inter-grading forms in all degrees are known. The whole question seems to be one of the relative time at which specialized substances are formed in the cytoplasm of the germ-cell or early blastomeres, or at least of the time such substances are segregated in cell division.

In cases of determinate cleavage, the cleavage planes may follow with surprising accuracy along predetermined paths so that each blastomere has definite characteristics and is destined to produce only certain tissues of the embryo. In the tunicate, *Styela*, for example, Professor Conklin has shown that if one or more blastomeres of the two- or four-cell stage are injured so as to prevent their further development the remaining blastomeres develop as usual, giving rise only to the special group of tissue-cells they would have produced had the destroyed cells remained in place in a normally developed embryo.

In some cases, however, a blastomere that under certain conditions gives rise to only a half embryo may under other circumstances produce a complete embryo, thus showing that it still contained all the essential ingredients. If one of the first two blastomeres of a frog's egg is destroyed, for example, the remaining one, provided it lives and remains undisturbed, develops into a half embryo. But if the uninjured blastomere is inverted after the operation, or if the injured blastomere is cut completely away instead of being killed and left in place, a rearrangement of the contents of the remaining blastomeres occurs and a small normal embryo subsequently develops. This process is sometimes called *post-generation*, but labeling it thus, of course, explains nothing. The significant thing is that even in cells which have

undergone a certain degree of particularization toward building a special part of the body there still reside all the potencies required to form the complete organism.

Early Cleavage in Man Probably Indeterminate.—Before leaving the topic of determinate and indeterminate cleavage it should be observed that the determinate type is not, as one might suppose, restricted to the most complex animals, such as the vertebrates. On the contrary these forms are known to exhibit the indeterminate type. Even in the case of man the evidence is that the early cleavage is indeterminate. It is possible that so-called identical twins originate as blastomeres which, having

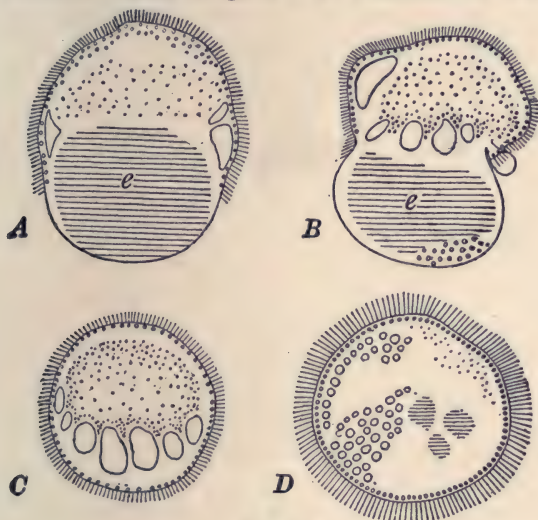


FIG. 16

Development and differentiation in the absence of cell division, in *Chatopterus*. (From Lillie.) *A, B, C*. Ciliated, uninucleated, unsegmented eggs, about twenty-three hours old. *D*. Ciliated unsegmented egg about twenty-eight hours old; most of the endoplasm has been consumed. *e*, Endoplasm.

become isolated in the two-celled stage, develop separately each into an individual. Another idea of the origin of identical twins, however, is that although they are derived from the same ovum, the divorcement of the two individuals takes place much later than the two-celled stage, through the suppression of the original axis of development and the establishment of a new one on each side of it.

Cleavage not the Fundamental Factor in Development.—

When one reviews the various lines of evidence it is clear that the mere matter of cleavage alone does not seem to be a factor of fundamental importance in development. The outcome is rather the expression of the original organization of the egg. This is well exemplified in an experiment by Professor Lillie on the eggs of a marine worm (*Chætopterus*). He succeeded in artificially inhibiting cleavage while at the same time securing the formation of a larva (Fig. 16, p. 59). Although there was absence of cell divisions the embryo formed external cilia for locomotion and certain other characteristic structures. Various pressure experiments illustrate the same fact. The eggs of some animals when subjected to a deforming pressure between glass plates or in glass tubes may have the direction of the cleavage planes markedly altered. Instead of forming the normal spheroidal group of blastomeres in the eight-cell stage, the cleaving egg of the sea-urchin, for example, may be forced to produce them in the form of a flat plate, yet when the latter is released from pressure it develops into a normal larva. In such cases, certainly, the cleavage furrows are not of prime importance in marking out germinal areas, and each blastomere must retain samples of all substances necessary to build up a complete individual.

One Individual from two Eggs or two Blastulas.—Not only can the experimenter secure in some cases several individuals from one egg which was originally destined to produce a single individual, but he can also accomplish just the reverse. The coalescence of parts of two eggs or even of two complete eggs has been brought to pass in such forms as the sea-urchin, with the result that a normal larva was formed—of giant size when the fusion was between two whole eggs. Likewise two blastulas, even of different species, can be made to fuse to form a single larva although there is frequently a tendency for some parts to be double.

Metabolic Gradients; Differential Susceptibility.—Professor Child has shown in numerous studies extending over a period of twenty years or more, on a wide range of animals, that the developing individual, in bilaterally symmetrical forms, has a marked polarity, with different rates of metabolism at different points along the longitudinal axis of the body. In the early embryo the developing head end always shows the highest rate of activity. This activity gradually diminished toward the pos-

terior end. Child has also shown that the more active a region is, the more susceptible it is to adverse chemical or physical influences. He found that by applying any one of various depressing agents at the appropriate stage of development, characteristic defects can be produced at will. The differing susceptibility of various regions at different stages of development is responsible for differences in the nature and magnitude of the result. Since

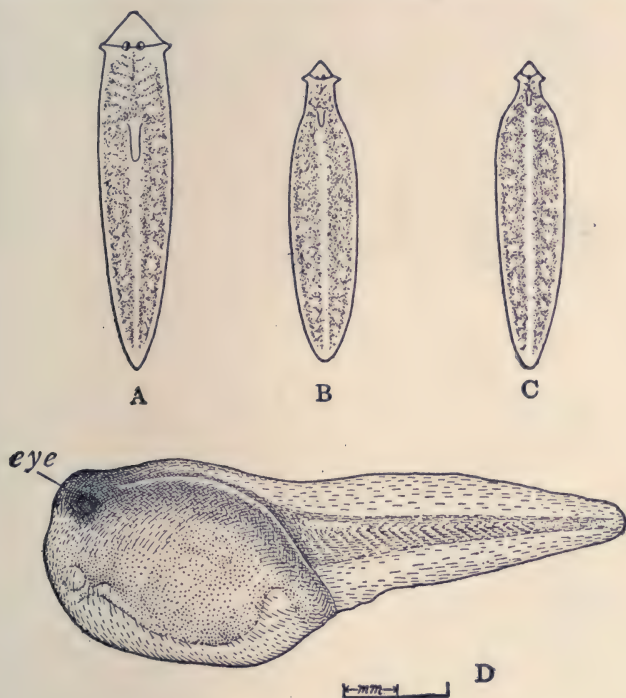


FIG. 17

A, B, and C are illustrations (from Herrick after Child) of planarian worms in process of regeneration after transverse section. A shows an approach to the normal form under standard laboratory conditions; B and C illustrate different degrees of retardation of head development under conditions which depress or inhibit growth. In B the two eyes are closer together than normal, and in C they have fused in typical cyclopean form.

D illustrates a cyclopean frog tadpole (from Herrick after Bellamy, 1919). This egg was treated with lithium chloride for three hours in the early gastrula stage. The development of the eyes was partially inhibited and the two eyes are fused in the median plane and reduced to a small vestige.

the rate of oxidation gradually diminishes along the gradient from the region of highest activity, Child holds that differences in oxygen supply probably play a very important part in the local metabolic differences. Figs. 17*A, B, C*, p. 61, show planarian worms regenerating heads after decapitation. In *A* the worm was kept under standard laboratory conditions and the head has regenerated normally. In *B* and *C* the individuals were kept under

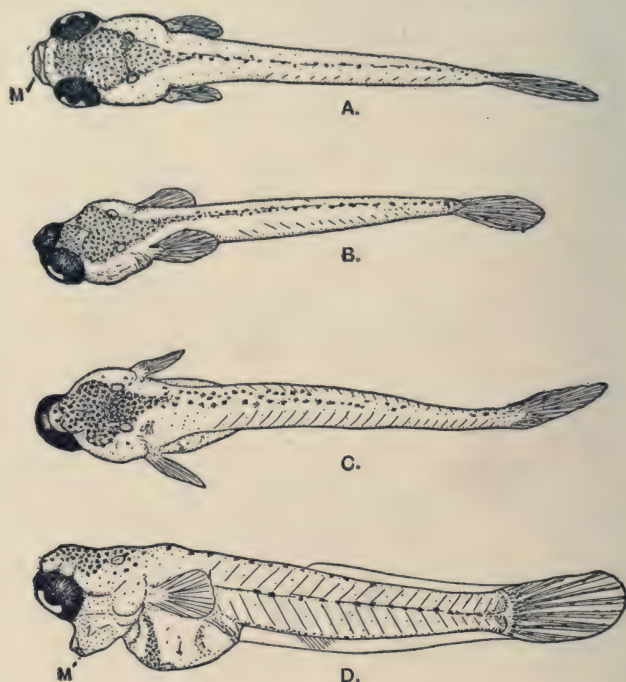


FIG. 18

Young of the marine minnow, *Fundulus heteroclitus* (after Stockard). *A*, normal larva; *B*, larva with the two eyes joined and occupying the position usually taken by the mouth; *C*, dorsal view of a completely cyclopean larva, with single antero-median eye; *D*, side view of the same showing the ventral mouth, *M*. The monstrosities were produced by subjecting the developing embryos to the influence of magnesium salts dissolved in sea water.

conditions which depress or inhibit growth so that head development has been retarded in different degrees; in *B* the eyes are abnormally close together and in *C* they have fused into one.

Experimental Production of One-Eyed Monstrosities.—

Many interesting experiments might be cited showing the production of particular or restricted effects due to alterations in external conditions of development, but one or two further illustrations must suffice. Professor Stockard found that when, at a certain critical period, the developing eggs of *Fundulus*, a common sea minnow, were subjected to the action of various magnesium salts dissolved in sea water, a large percentage of them—as many as sixty in one hundred individuals—developed a single median eye instead of the ordinary pair (Fig. 18, p. 62). He and others have also secured cyclopean monsters through the use of alcohol, ether, and certain other reagents. Thus Bellamy obtained such cyclopia in frogs by applying a solution of lithium chloride during very early development (Fig. 17D). Different degrees and kinds of cyclopic defects—complete, partial, “hour-glass,” and the like—are obtainable, depending apparently upon arrests at particular stages of development. Entirely different eye anomalies and other abnormalities may be secured if the same means used in producing cyclopia are applied at a different stage of development. Inasmuch as the same type of defect may be produced by any one of a number of different chemical or physical means, it is clear that the response is not specific with respect to a given agent.

Production of Double Monsters.—Incomplete separation of blastomeres usually results in the formation of double monsters, that is, Siamese twin-like forms. By keeping the two-celled stage of the frog upside down such monstrosities of varying degrees of duality may be obtained. The same effect has been produced in the case of certain salamanders by tying a hair around the developing mass.

In a recent report of experimental studies on twins, double monsters and other deformities, and on interactions among embryonic organs, Stockard, like Child, attributes much importance to reduction of oxygen supply at critical stages of embryonal or organal development in causing arrests which result in the production of abnormalities. He shows that by temporarily lowering the temperature and thereby reducing the rate of oxidation, or by directly cutting off the supply of oxygen, the normal continuous course of development of the embryo or of some embryonic part may be interrupted, with the result that characteristic suppressions or distortions may occur. Interruption of

development during late cleavage, for example, results in the production of a considerable number of twins and double individuals.

Likening the developing animal body to the growing plant shoot, Stockard has given a very clear interpretation of many of the structural reactions, normal and abnormal, which may be observed. In a shoot of the ordinary garden privet, for instance, under certain conditions one finds a rapidly growing end bud and, in the axis of each leaf, a resting axillary bud (Fig. 19, below). As long as the apical bud is growing vigorously the axillary buds remain dormant, but let the terminal bud become inactive or be injured or removed, and the axillary buds

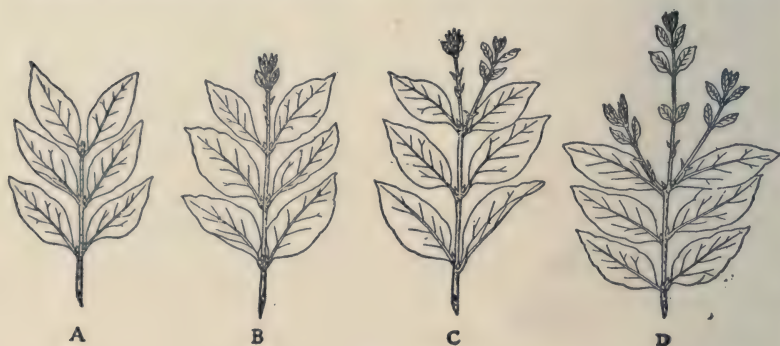


FIG. 19

Showing the growth of shoots from the apical and axillary buds of a plant stem. A, all buds resting; B, the usual single apical shoot; C, the apical and one upper axillary bud growing; D, the apical and both upper axillary buds growing. (After Stockard.)

begin to grow (Fig. 19B, C, D). If the terminal bud is injured so as to grow more slowly, as long as it keeps growing the activity of the axillary buds will be correspondingly held in check. In other words, a certain competitive pressure exists among the buds on the stem, and extension of the axillary buds is ordinarily inhibited because of the very fact that the apical bud is growing vigorously.

In the early embryo of ordinary animals there is similarly a linear axis of growth which leads off in development. But if, as various embryologists, notably Child and Stockard, have demonstrated, the original growth axis is caused to slow down

or become inactive by any of several well known physical or chemical means, then one or more new axes arise. Thus apparently competitive processes similar to those in the plant stem are at work in the developing animal. As long as the original axis maintains vigorous activity it holds in check the initial growth tendencies of other regions, but once it is inhibited or is prevented from coming into active expression then one or several new growth points may manifest themselves and establish new axes. In this way Stockard explains the origin of the twins, double

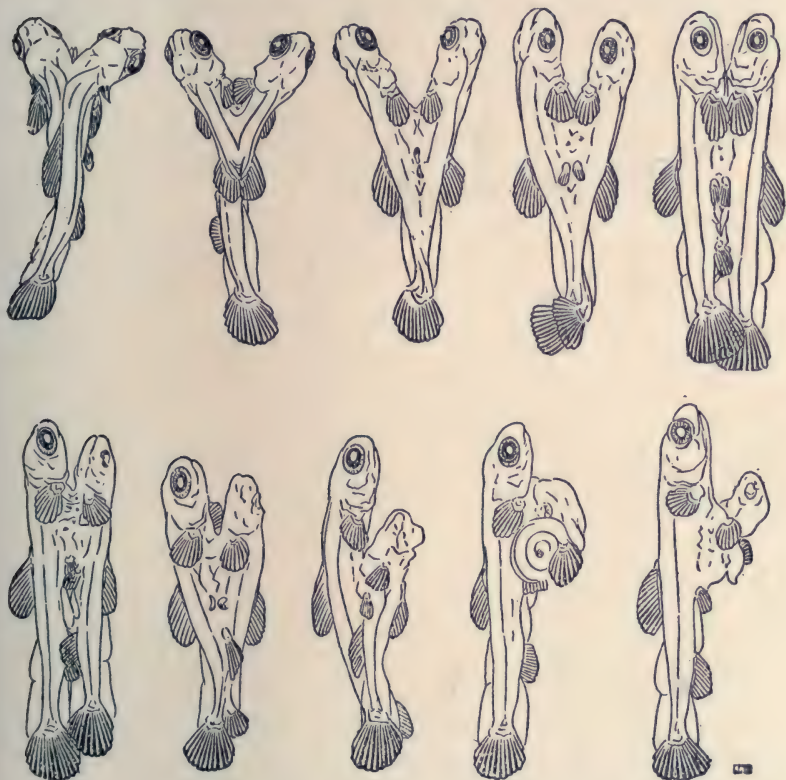


FIG. 20

Upper row: A series of double individuals in which the two components are equal in size and both are structurally normal. Lower row: A series of double individuals in which the components differ in size. The larger component is normal and the smaller more slowly developing component is always deformed. The degree of deformity varies directly with the difference in size between the components. (After Stockard.)

embryos, and other multiple conditions he has so successfully produced in his various experiments. In fish he finds that the degree of separation of the two components of double monsters depends upon how far apart the two new growth points arise in the ring-like region (*germ-ring*) of greatest formative activity. He has secured graded series of fish ranging from individuals with slightly separated heads on single bodies through specimens with two bodies and common tail to completely separated twins, (Fig. 20, upper row, p. 65).

When one of the originating buds chances to be more favorably located than the other, however, it grows at normal rate and develops normally while the less favored one grows more slowly

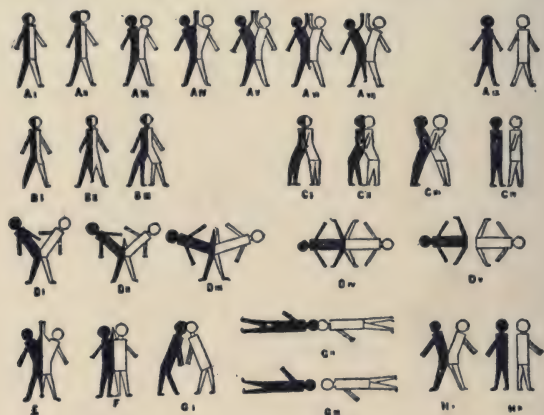


FIG. 21

Diagram of double monsters in man. (After Wilder.)

and always develops abnormally. And the latter shows deformities in direct proportion to its degree of suppression (Fig. 20, lower row). Stockard believes that such structural reactions are universal among developing vertebrates. Since in man there are many cases on record of dual monsters of different degrees of completeness from two-headed forms to two almost complete individuals, as well as individuals joined to one another in various positions, it is reasonable to suppose that factors similar to some of the foregoing have contributed to their production. Fig. 21, above, shows in a schematic way some of the possible twin, or partial twin, monstrosities which may exist in man. Such double forms are always of the same sex.

Other Types of Deformity Due to Retarded Development.—

Not only is retardation of the rate of development the dominant factor in the production of twin monstrosities but it is responsible as well for innumerable deformities which may arise in single embryos. In the words of Stockard, "all unfavorable treatment whether chemical or physical tends primarily to slow the rate of development, and the developmental stage at which the slowing occurs determines the type of deformity." Applied at a very early period of embryogeny the adverse influence may cause the formation of twins and double individuals; applied slightly later, double individuals are never produced but various abnormalities of the eyes are the prevailing defects; still later, gross deformities of the eye do not result, but some other actively developing organ is the part affected. Thus he has succeeded in locating the respective developmental periods during which such organs as the eye, the heart and blood-vessels, the mouth, the gills and the liver may be greatly modified or suppressed. He believes that his results warrant the conclusion, "that there are in the development of all or many organs certain periods at which those organs are peculiarly sensitive to any unfavorable condition which may act upon the embryo. Further it may be emphasized that the peculiarly sensitive period is very close to the actual moment of origin of the organ in question. After an organ has arisen and passed through the earlier stages of its development it becomes less inclined to suffer radical modification in its manner of development as a result of unfavorable conditions. After it is completely formed it is quite resistant."

The Development of One Part may Condition that of Others.—In embryological development one part may very materially condition the development of others which are wholly unrelated to it in origin. Thus the sensory parts of the eyes originate as a pair of bulb-like outgrowths from the sides of the forebrain, known as the optic vesicles (Fig. 22*B*, p. 68). As each optic vesicle develops it becomes marked off from the brain by means of a definite stalk, and through elongation of this stalk the bulb soon comes into contact with the external ectoderm of the embryo. At the point of contact the ectoderm thickens to form the crystalline lens of the eye (Figs. 22*B*, *C*). Although a lens may sometimes form, if by any means the optic vesicle is prevented from touching the ectoderm, it frequently will not. Experiments in certain amphibians show that if the optic vesicle

is transplanted beneath the ectoderm at another place in the embryo, notably in the head region, so specific is this lens-forming stimulus of the vesicle, that the ectoderm which comes into contact with it forms a definite lens. In other words, epidermis that does not normally give rise to lens will do so if brought into contact with the optic vesicle. Such an experiment raises anew the question of how much an organ which develops in a given region of an animal is a self-differentiating structure, how much it owes its occurrence to contact and other stimuli.

Regeneration of Lost Parts.—The regeneration of lost parts

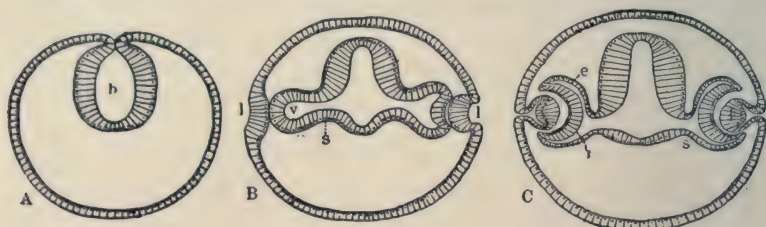


FIG. 22

Diagram showing stages in the formation of the retina and the crystalline lens (after Hertwig). In A the brain (*b*) has closed in; in B the optic vesicle (*v*) has reached the ectoderm and the lens (*l*) is forming (farther advancement shown on the right side); in C the double-walled optic cup (the inner layer of which becomes the retina) is formed and the lens is about ready to detach itself from the outer ectoderm; *s* marks the optic stalk.

by animals and plants is a phenomenon that must also be reckoned with in a discussion of the mechanics of development. That many plants have a practically unlimited capacity for repairing mutilations is a fact familiar to every one. A slip cut from a geranium readily regenerates the missing parts and becomes in a short time a complete plant. Likewise, the cut end of a limb of a tree heals, and sends forth new branches or leaves. This capacity of pieces of plants to give rise to new plants has long been known. It was supposed by older investigators to be confined to the plant kingdom and was in consequence used as a test to determine whether an organism was a plant or an animal. Thus in 1750 Trembly experimented on *Hydra* to determine whether the new creature which he had found was a plant or an animal. *Hydra*, we know now, is a simple multicellular animal which has remarkable power of regenerating a complete indi-

vidual from fragments cut from its body. It, like various other simple animals, also reproduces at times by budding off young individuals from its own body.

Following Trembly other investigators experimented further and discovered that the same power of regeneration existed in other animal forms, such as earthworms, fresh-water worms, snails and newts. The results of Spallanzani, indeed, demonstrating that a snail regenerated a lost head, called forth scathing criticism from his contemporaries, who considered it beyond belief that this animal could develop a new head and all the organs contained therein. Even to-day we may well marvel at the capacity some animals display for making good lost parts. Thus in the starfish the body may be torn completely in two and each half will regenerate the missing portion. In one kind of starfish, indeed, a single ray can generate all of the missing parts. Instances are known in this form where from a wound in one arm a new individual has budded forth (Fig. 23*A*, below).

Again the whole viscera of some animals will regenerate if



FIG. 23

A. Starfish (*Linckia multififormis*) with four new arms springing from the end of one arm (from Morgan after Sarasin).

B. Hydroid (*Tubularia*) regenerating a head at each end of a piece of the stem suspended in water (from Wilson after Loeb).

removed, and the leg or eye, or antenna of a crab or crayfish if amputated will be regrown. A salamander has had its tail cut off eight times in succession, and the eye-bearing tentacle of a snail has been removed twenty times, yet after each mutilation the missing organs have been produced anew. In man and the higher vertebrates regeneration is much more limited in extent, being confined for the most part to such activities as

the healing of wounds, the replacement of tissue-elements in injured internal organs, the production of new blood cells, the renewal of hairs, and other minor regenerative operations.

Morphallaxis.—In regeneration experiments, because of its wide distribution and the ease with which it may be obtained and kept under laboratory conditions, as well as on account of

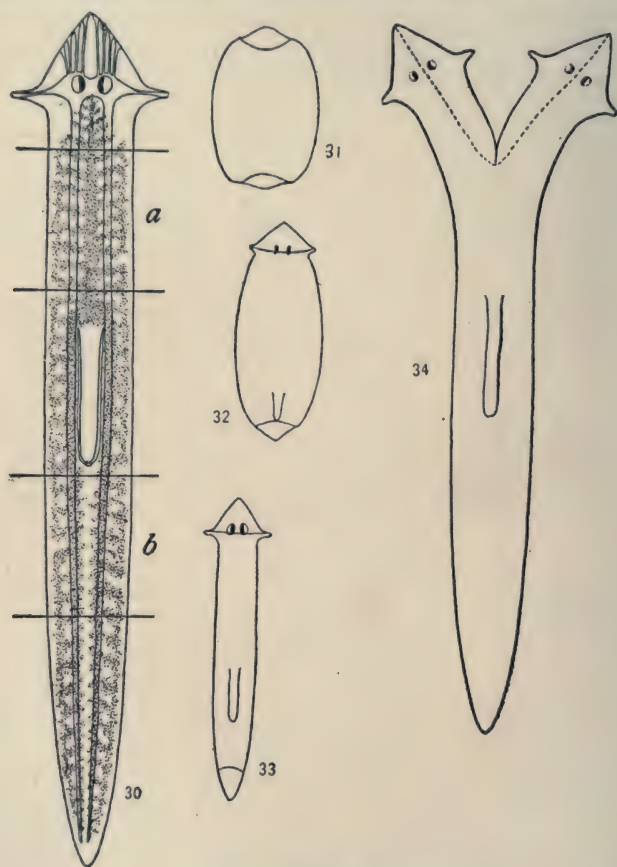


FIG. 24

Illustrations of regeneration and reconstitution in *Planaria dorotocephala*, a planarian worm (after Child): in 30, *a* and *b* indicate two regions cut out for reconstitution; 31 to 33 show stages of reconstitution; 34, a two-headed planarian produced by partial longitudinal splitting (dotted line indicates approximate boundary between old and regenerated tissue).

its remarkable regenerative capacity, *Planaria*, a small flatworm of which there are many species, has been widely used (Fig. 24, p. 70). If an ordinary planarian is split at the front end without entirely dividing the body, the two lobes thus produced will each become a perfect head (Fig. 24). It may be cut in almost any direction or cut into several pieces and each will remodel itself into a complete, though smaller, individual (Fig. 24). The restoration is accomplished partly through a reconstitution in which the old tissues are remolded into new structures, and partly through a real regeneration or growth of new parts. The process which involves the transformation of an old part into a complete new organism is known as *morphallaxis*.

If the head of a planarian is cut off too far forward, however, instead of a new body, a new head may grow out in the opposite direction and thus give rise to an individual with two heads and no body. Similar results have been obtained with other forms. The earthworm, for example, if cut too near the tail end may regenerate a new tail toward the front end instead of the head necessary to a complete animal. As to the exact meaning of this there is much debate among experimentalists themselves and for our purposes we need not go into it beyond noting the fact.

Some remarkable examples of restitution of body form and function have been found by Professor H. V. Wilson among sponges and hydroids, both groups of which are simple, aquatic animals. These organisms were cut into small fragments and then pressed through the meshes of fine bolting cloth. In this way the flesh was broken up into individual cells or very small cell aggregates. Shortly after the operation many of the isolated elements were observed to have fused together into lumps or sheets of tissue. Soon larval stages arose very similar to the typical normal larva. Ultimately new complete adults developed. Even cells from different individuals could be made to unite in this way to form a new organism. Garbowski found likewise that if cells taken from a number of different blastulas of the sea-urchin were pressed together they would sometimes form aggregates which developed into normal larvæ. In such experiments the evidence indicates that the individual cells of the new organism may form part of an entirely different organ or tissue from what they did in the original animal; that a given cell is not always irrevocably committed to the duties of one place

alone in an organism. Both Huxley and Galtsoff maintain, however, that in such experiments with sponges while certain of the dissociated cells become somewhat simplified, they do not return to a truly "dedifferentiated" or embryonic state. These investigators believe that, in their experiments, body restitution was accomplished by a sorting out again of the different kinds of cells into their proper places in the organism, together with a certain amount of redifferentiation of the individual cells.

Substitutions of Organs.—Further significant facts are brought to light when the normal conditions which surround a regenerating form are altered. If *Tubularia*, a simple marine animal, be decapitated it will regenerate its "head," that is, the portion bearing mouth and tentacles. If, however, the animal be cut off at both ends and that which bore the head is buried

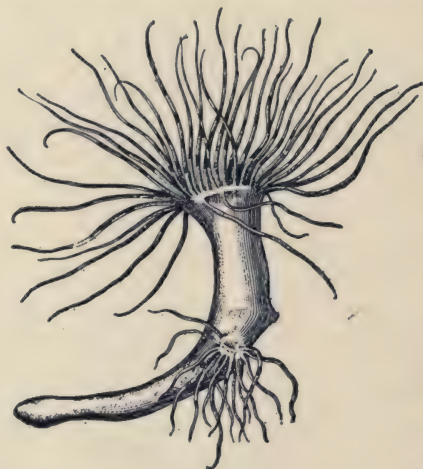


FIG. 25

Polyp (*Cerianthus*) producing tentacles from the lower edge of a wound in the side (after Loeb).

in the sand a new head is regenerated at the free or foot end and a foot at what was originally the head end. If both ends are buried in the sand neither regenerates a head, and if the body is suspended free in the water both ends develop heads (Fig. 23B, p. 69). Such a development of a part different from the one removed is known at *heteromorphosis*.

Certain experiments which have been performed on the sea-anemone, *Cerianthus*, are instructive in this connection. Although having somewhat the appearance of a plant, *Cerianthus* (Fig. 25, above), is really a simple animal. The body is essentially a double-walled sac with a tentacle-crowned head region at one end and a so-called foot at the other. In the center of the circlet of tentacles is the mouth. If an incision is made in the side of the animal new tentacles may spring up around it as if surrounding a mouth and such new tentacles behave toward food exactly like the tentacles surrounding the old

mouth (Fig. 25). If the tentacles of the two different systems are stimulated simultaneously with the same piece of meat a struggle follows, each attempting to draw the meat toward its own mouth region.

An interesting example of regeneration which seems to be conditioned by the presence or absence of certain internal parts correlated with the structure removed has been seen in various crustacea, among them the prawn (*Palæmon*). When the eye is removed a new eye regenerates but if the eye-stalk is divided very close to the head so that not only the eye but the optic ganglion at its base is also removed, then not an eye but an antenna grows out from the wound (Fig. 26, above).



FIG. 26

Diagram showing brain, eye and an antenna in the prawn (*Palæmon*) (after Herbst). The antenna has regenerated in place of a removed eye.

Animal Grafts and Transplantations.—Closely allied to the subject of regeneration among animals is that of grafting. It is not an uncommon experiment in laboratories to take two different animals, indeed perhaps different though allied species of animals, and graft them together to form a composite. The grafting of lower forms like hydra or like the earthworm is comparatively easy. The front half of one earthworm really grows fast to the tail half of another if they are fixed firmly together for a short time.

Among the lower vertebrates experimental transference of parts of the body such as the grafting of the front end of one tadpole on to the tail of another has been accomplished. Professor Harrison, one of the pioneers in this interesting field of experimentation, succeeded in securing a composite frog (Fig. 27, p. 74) of two entirely different species by grafting their tadpoles together in this way. The fact that the two species differed materially in color markings added to the visible clearness of the experiment. The resulting frog seemed to have perfectly normal instincts and powers of coordination. Crampton obtained

just as striking results by grafting together the pupæ of different species of the larger moths.

Through experiments in transplantation, Harrison has been able to clear up, among other things, several disputed points regarding the relation between nerve centers and organs. In his own words: "Limb buds of tadpoles, when transplanted to various parts of the body of normal individuals, develop normally and acquire usually a complete or partially complete system of peripheral nerves, which have normal arrangement and are



FIG. 27

Grafted frog embryos, head and anterior end, *Rana sylvatica*, posterior part, *R. palustris*. Composite frog formed from such a graft. (After Harrison.)

connected with the nerves of the host supplying the region in which the limb is implanted. The nerves are not formed *in situ* in the transplanted limbs but grow into them from the nerves of the host." Others of his experiments show also that functional activity of the part a nerve fiber is to supply or of the fiber itself, is not necessary for the development of the fiber, but that peripheral fibers originate wholly from extensions of

the ganglion cells. A right limb, however, once it has begun to differentiate, remains a right limb even if transplanted to the left side of the body.

In the field of pathology much valuable information is being gained at present about the cancer problem by transplanting tumor cells from individual to individual, and generation to generation of experimental animals.

The capacity for grafting in higher vertebrates like man, for example, is much more restricted, yet here we are familiar with such operations as skin grafting and the transfusion of blood. However, even in mammals, in attempting to extend the bounds of modern surgery some remarkable cases of transplantation of organs from one animal to another of the same species have recently been accomplished. Various internal organs, such as pieces of blood-vessels, kidneys and other structures have been replaced in one animal by corresponding organs removed from another animal of the same kind. Much nonsense, however, has of late been going the rounds of the popular press about the transplantation of non-human tissues such as "monkey-glands" into man. While bits of tissue transplanted from one species of mammal to another may occasionally become attached and temporarily reestablish their circulation, they soon undergo destruction by a process apparently akin to digestion and are replaced by scar tissue. Even for successful blood transfusions from one human being to another, since there are four distinct types of human blood, the blood of the donor must be of the same type as that of the patient.

Culture of Tissues Removed from the Body.—In spite of the wonderful regulative and regenerative capacity manifested by some animals or some parts, on the other hand, some remarkable cases of persistence of specialization or differentiation once established are known. In recent times much attention has been given to the culture of tissues removed from the body. It has been found that if such tissues are carefully removed so as to avoid infection, kept at suitable temperature in lymph or appropriate nutritive fluids, and transplanted from time to time into suitable new media, they may be kept alive and growing, not only for several days or weeks, but even for years. While adult tissues may be so manipulated the most instructive results have been derived perhaps from bits of tissue isolated from young embryos. In this way tissues which normally develop

in internal positions that can not be inspected can be exposed and observed to undergo more or less of their characteristic differentiation under the microscope. Thus, for instance, pieces of embryonic tissue about to give rise to nerve fibers may be isolated and studied in the actual process of forming such fibers by the outflowing of protoplasm from the central cells. Likewise, masses of cells clipped from regions which would give rise to muscle in the normal embryo, still retain their impulse toward muscle formation, and although placed under totally different conditions nevertheless differentiate into muscle fibers showing typical striations. In favorable preparations they have been seen, after two or three days of development, to undergo contractions.

At the Rockefeller Institute in New York City tissue removed from the heart of a chick embryo has been thus cultivated apart from the body for more than fourteen years and is still true to type and growing as actively as ever. Speaking of this material at the end of ten years of its growth, Professor Wilson in his book on *The Cell* says: "More than 30,000 cultures have thus been obtained from an original small fragment, the cells having passed through about 1900 generations; and had it been possible to preserve all the cells thus produced their combined volume to-day would be far larger than the sun." Had the original chick from which this tissue was taken lived and grown to maturity it would probably have been dead long ago since the natural length of life in the fowl is ordinarily only some six or seven years.

Senescence and Death Apparently Not Inherent in Living Matter.—Such facts as these together with the observation upon the almost limitless powers of continuous growth of tumors transplanted from generation to generation, and the apparent deathlessness of varidus protozoa, to say nothing of the cultivation of plants by cuttings through innumerable generations without impairment of vigor, open up the great question of old age and death. They raise a doubt that senescence and death are inherent in all living matter. These twin abhorrences of man seem rather to be due to secondary conditions. Needless to say such matters have long been subjects of inquiry by biologists. Opinions regarding the causes of senescence are varied. We can not review them here. The outstanding fact is that in tissue cultures even highly specialized cells can live on apparently indefinitely, at least far beyond their normal span of life.

Professor Child maintains that senescence is due to decrease in the rate of metabolism and that if in one way or another we can remove "the structural obstacles to metabolism"—the inactive constituents the accumulation of which is incidental to the vital process in complex organisms—a rejuvenescence results. This opinion is perhaps as near the truth as any of the hypotheses in this field. At any rate, Child has given us the best experimental evidence of keeping certain simple animals perpetually young, or of making them grow "young" again once they have aged. For example *Planaria velata*, a simple flatworm, passes through its entire life cycle in from three to four weeks. The young animals at first grow rapidly but the rate of growth gradually decreases until, having attained a length of about fifteen millimeters, they cease to feed and gradually become inactive. Disintegrative processes set in and finally the body automatically breaks up into small bits. Each fragment eventually reconstitutes itself into a new, physiologically young animal which repeats the life history. This is the only form of reproduction Child observed in this form during more than thirteen years of study. In experiments with a stock of these animals lasting over three years, he found that by controlling nutrition he could seemingly control the aging of the animals. By keeping them without food for a time he could make them diminish in size and become in appearance and in physiological reactions like young individuals. He could even reduce them in this way to less than one-fourth their original size and, by proper nutritive control, he could maintain them at any age-level he desired. Thus, he apparently effected an actual rejuvenescence. While a portion of his laboratory stock kept under conditions of full nutrition passed through thirteen generations, he was able to maintain his experimental animals, taken from the same stock in a condition of physiological youth all this time, exhibiting all normal activities except reproduction. In other words, in a form which runs its natural course in some four weeks he was not only able to retard or inhibit senescence for over three years but could even at will make the organism become more juvenile.

Speaking of man Child says: "For his high degree of individuation man pays the penalty of individual death, and the conditions and processes in the human organism which lead to death in the end are the conditions and processes which make man what he is." Professor Pearl's view of senescence as the

loss of the normal interbalance of cells is also interesting and suggestive. He points to the fact that a higher organism is built up of mutually dependent cells held in very complex equilibrium. Pathological changes in any part ultimately upset this balance beyond the point of repair.

Internal Secretions as Factors in Development.—Still to be reckoned with, in the back-boned animals, among the factors of development during the post-embryonic period which can not be reduced strictly to original internal impulsions in the cells of a particular part are the secretions from certain organs commonly called the *ductless* or *endocrine glands*. Since these secretions do not pass out through ducts as do the more familiar glandular products, but are directly absorbed from the tissues of the gland into the blood or lymph, they are often spoken of as *internal secretions*; they are also called *hormones* or “chemical messengers.”

The best known of the endocrine glands are the *thyroid*, the *parathyroids*, the *thymus*, the *pituitary body*, the *adrenals*, the *generative glands* and special areas of the *pancreas*. The secretions in question while necessary to the normal functioning of various parts of the body in the adult, are, from our present standpoint, of chief interest because they are also essential for normal development and growth.

The importance of the endocrine glands in regulating the activities of the organism is probably second only to that of the nervous system. They can stimulate or inhibit the activity of some organ or tissue in a part of the body far distant from the source of the secretion itself. While the modest achievements of the biologist, the pathologist and the biochemist toward an understanding of the nature and functions of the internal secretions do not warrant the wild exploitation of this new knowledge seen under such captions as “The Chemistry of the Soul,” “Rejuvenescence through Monkey Glands,” or any other equally sensational title, still, the facts alone, unmagnified by the imagination, are certainly striking. Many physical and even psychic abnormalities in man are being traced to hereditary or acquired deficiencies of the endocrine glands, or to upsets of their normal interrelations at various physiological periods in the individual. Atrophy or hypertrophy of such a gland may produce profound effects in the furthest reaches of the body. Our height, the general form and external appearance of

our body, whether slender or broad, the length of our arms and legs, the shape of our face, the quality of our voice, the distribution of hair or of fat on our body, and even our emotions are in greater or less measure conditioned by the relative functionings of our various endocrine glands during earlier development and later life. And doubtless the amount and quality of the internal secretions in various family strains are as much the expression of hereditary factors as are many other individual characteristics.

The thyroid, situated in the neck region, consists in man of two parts, one on either side of the "Adam's apple" and wind-pipe, usually joined by a narrow band of tissue. It produces a secretion which is of great importance in maintaining a normal balance of the nutritional and growth processes. It seems to play a prominent part in controlling the rate of the body metabolism. If the thyroid is diseased the whole body may be affected. Over-abundance of thyroid secretion (*hyperthyroidism*) increases the heart beat, causes higher temperature and in general speeds up the body activities. Thyroid insufficiency (*hypothyroidism*), on the other hand, leads to decrease in metabolic rate, lowering of temperature, sluggish muscular movements and mental dullness; and the skin, especially of the face and hands, may become puffy from the presence of underlying mucous fluid (*myxedema*). Inadequate development or atrophy of the thyroid in the young child produces a condition known as *cretinism*, characterized by arrested growth and deficient mental development, (Fig. 28, facing p. 80). Such children, if taken in time, often show remarkable improvement, both in body and mind, after the administration of thyroid extract.

As affecting development some interesting experiments have been performed upon tadpoles with thyroid. Guternatsch discovered that tadpoles fed on thyroid are forced into premature metamorphosis so that they quickly turn into miniature frogs, sometimes no larger than a fly. Allen, on the other hand, has shown that if a young tadpole is deprived of its thyroid it is unable to become a frog, although it may continue to live and may grow beyond the usual size of a tadpole. If at any time such a tadpole is fed thyroid, however, it promptly undergoes metamorphosis.

The active principle of the thyroid hormone has been isolated by the biochemist Kendall in the form of an organic iodine com-

pound which he calls *thyroxin*. Thyroxin contains no less than sixty per cent. of iodine. So-called endemic goiter, manifested usually as a swollen condition in the front part of the neck, is due to a diseased and enlarged state of the thyroid gland. Goiter is very common in the Great Lakes region of our own country. That iodine insufficiency is an important factor in its causation is indicated by the fact that many remarkable cures have been affected through the administration of small quantities of inorganic iodides, commonly sodium iodide, in food. So effective is this treatment for the prevention and cure of this form of goiter that in some places whole school communities now take the sodium iodide treatment for a few days each year as a matter of hygienic routine. Such iodine administration should be undertaken, however, only under competent medical supervision since to certain individuals who have what is known as toxic goiter, iodine may act as a poison.

The *thymus*, an organ in the throat region near the thyroid, is commonly regarded as a ductless gland although its exact function is a matter of debate. Since it attains its maximal size and activity in early childhood the inference is that it functions most actively in the young developing organism. There are indications that one of its functions is to hold in check for a time the development of the reproductive organs. In castrated animals, for example, the thymus enlarges and, on the other hand, removal of an animal's thymus, though delaying growth, may accelerate sexual development. Surgical removal of the thymus, while not necessarily fatal, as is total removal of the thyroid, is said to produce a disordered development of the skeleton similar to that seen in a child with rickets. Young dogs in which the thymus had been completely removed developed a softening of the bones similar to that which characterizes a disease known as *osteomalachia*.

The *pituitary gland* or *body* projects downward from the base of the brain into the floor of the skull. As in the case of the thyroid its complete removal in man or the dog results in death. It is divided into two parts, an anterior portion derived embryonically from the roof of the mouth, and a posterior lobe which grew downward from the floor of the brain. The two parts have different functions. The anterior lobe affects stature; over activity probably leads to gigantism, insufficiency, to dwarfing. Partial removal of the anterior lobe in young experimental

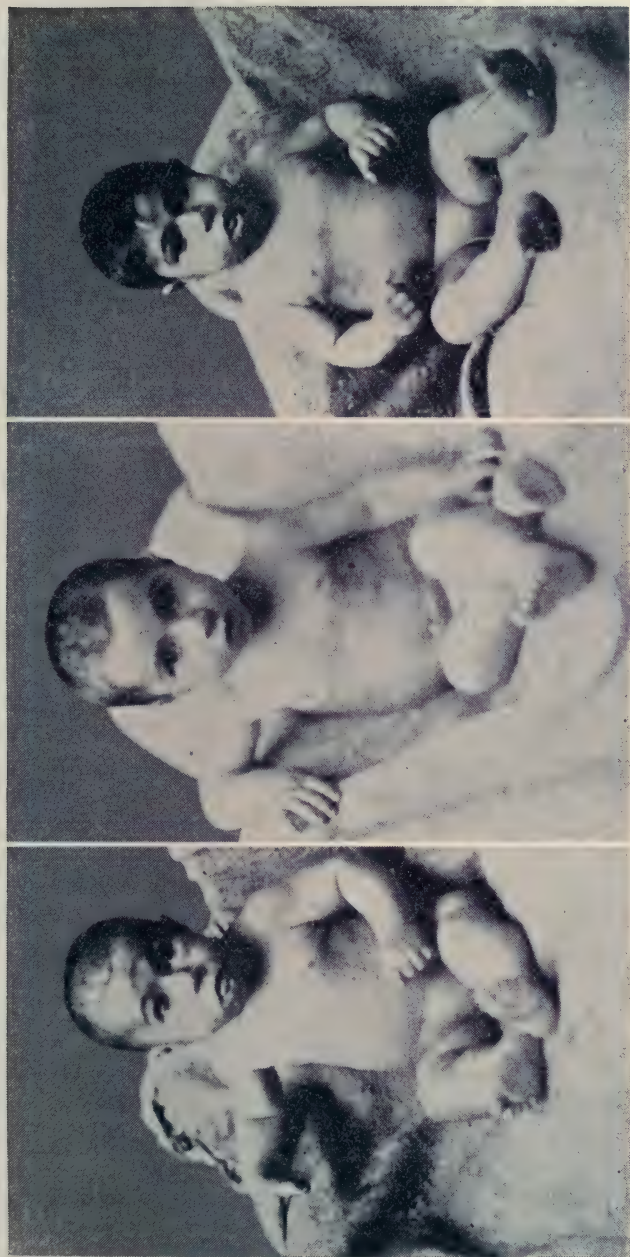


FIG. 28. Cretinism due to thyroid insufficiency (after Schlapp). Three views of the same child: before treatment; after three weeks of thyroid treatment; and after treatment had been discontinued six months.

animals results in a marked stunting in size (Fig. 29A, below). Autopsies on various human giants, on the other hand, have revealed tumorous and enlarged pituitaries. If the excessive secretion begins in youth while the growth zones of the bones are still unossified, lengthening of the bones, particularly of the arms and legs, occurs, and a form of gigantism is apparently the outcome; but if such overactivity does not appear until maturity a different type of enlargement occurs in certain bones, notably those of the hands, feet, and face, and a condition of deformity known as *acromegaly* results. The posterior lobe of the pituitary seems to influence the sugar metabolism and fat formation of the body and if its secretion is deficient in early



A

B

FIG. 29

A. Result of removing the pituitary body; dog at left is of the same age and litter as the other but it had its pituitary body removed at the age of two months (from Osborn after Aschner).

B. Result of removing thyroid and parathyroid glands; sheep at left is of same age (fourteen months) as the other but its thyroids and parathyroids were removed at the age of two months (from Osborn after Simpson).

life a type of infantilism results. Pigmentation in tadpoles depends in part, at least, upon the pituitary gland, since when it is removed the animals are albinic.

The *adrenal bodies*, located at the upper front edge of the kidneys in man, are another pair of ductless glands the secretion of which produces a profound influence on the structures and functions of the body. Each gland consists of two distinct parts,

a central *medulla* and a superficial *cortex*. The secretions from the parts differ in physiological action. That from the medulla, called adrenalin has not only been isolated in a pure state but has also been synthesized in the laboratory. It is widely used in medicine as a drug. In the body it is important in maintaining muscular tone; the proper amount keeps the blood-vessels suitably contracted and blood-pressure normal.

Insufficiency of adrenalin in the blood results in lowered blood-pressure, lack of muscular tone and the general loss of strength and "nerve" which is characteristic of neuresthenia, "shell-shock" and related ills. In general, adrenalin affects the same structures of the body that the sympathetic nervous system does; namely, the heart, blood-vessels, kidneys and other viscera, and the involuntary muscles. It is widely used in minor surgery because it constricts blood-vessels and thus checks bleeding. Tadpoles fed on adrenal gland become extremely light colored or "bleached," apparently because it produces contraction of the pigment cells. Injection of adrenalin into the blood leads to increase in the quantity of blood sugar.

Professor Cannon and his associates conclude from their experiments that under stress of such emotional states as pain, suffocation, fear or rage, the adrenals are stimulated to an increased output of adrenalin. Cannon calls attention to what he regards as the remarkable adaptive character of the reactions which follow in that they supply the body with muscular power to resist or carry out any of the actions that may take place under these emotions for the welfare or preservation of the individual. According to him the sugar of the blood—the most favorable source of muscular energy—increases in quantity; if digestion is in progress its activities are suspended and the blood is shifted to the organs immediately necessary for muscular exertion,—the lungs, heart and central nervous system; the blood becomes more coagulable; heart action becomes more vigorous; muscular fatigue is counteracted by the extra adrenalin; in brief, such fundamental readjustments are instituted as are favorable to great feats of strength or endurance—for fight or flight. According to Cannon's view, then, adrenalin is a chemical agent which cooperates with nervous factors in helping the body meet the emergencies of existence. His conclusions have not gone unchallenged; the physiologist Stewart, in particular, maintains that the effects in questions are attributable, not to excess of adrena-

lin, but to greater flow or altered distribution of the blood under the control of the nervous system. The two points of view, however, are not necessarily irreconcilable. Cannon, in fact, has never affirmed the supremacy of the chemical over the nervous factor but has merely maintained that the two sets of factors are coordinated.

The secretion of the cortical part of the adrenals has never been definitely isolated and is therefore not so well known as is adrenalin. Inasmuch as cortical enlargement (*hypertrophy*) of the adrenal is said to be associated with precocious sexual development, one of its functions seems to be concerned in some way with the development of the sex glands and with sexual maturity.

Complete removal of the human adrenals results in death. A serious malady in man, known as Addison's disease, characterized externally by bronzing or pigmentation of the skin is associated with pathological changes in the adrenals.

It has long been known that the generative glands (*gonads*) besides forming germ-cells also produce internal secretions which influence other parts of the body, especially the development of specific male and female characteristics. Much experimentation has been in progress with the lower animals in this connection in recent years and many interesting facts determined. In certain mammals such as the rat or guinea-pig, for instance, if the ovaries of a female are transplanted into a male which has been previously unsexed, the latter under stimulus of the ovarian secretions assumes a behavior like that of the female. Its hair and skeleton come to resemble more those of the female than of the male, and its rudimentary milk glands become enlarged to functional size. Again, Hisaw has shown, in the pocket-gopher (*Geomys bursarius*), that injection of ovarian material into males induces in them an absorption of a bar-like part of the pelvic bones which in untreated males persists throughout life, although such absorption normally occurs in young females as the breeding season approaches. If the ovary of a Mallard duck is completely removed, at the succeeding moult she takes on the very different plumage of the male. Likewise, if the ovaries are removed from very young hens they develop the more ornate plumage, the spurs, wattles, comb and larger size of the cock.

A remarkable experiment which reveals the importance of the sex-hormone in sex differentiation has been discovered by

Professor F. R. Lillie in his study of the "free-martin," a sterile female calf born as a twin to a male calf. In cattle when twins, one male the other female, arise, the blood-vessels in the fetal membranes of the two embryos may fuse in such a way that their blood intermingles. The male gonads develop ahead of the those of the female with the result that the male sex-hormone is the first to pass into the joined circulatory systems. It interferes with the growth of the ovary in the female causing sterility and modifying more or less profoundly various of her secondary sexual characters so that they tend to assume the male condition.

One can not, in even the most cursory review of the endocrine system, omit mention of the pancreatic hormone which controls the metabolism of the blood sugar. In certain diseased conditions of the pancreas the centers which elaborate this secretion are destroyed or injured, resulting in the disorder known as *diabetes mellitus* which is characterized by the loss of sugar through the urine. The news columns of our daily press have recently been so filled with announcements of the efficiency of the newly-discovered "insulin" as a remedy in diabetes that no further comment is necessary beyond pointing out that insulin itself is a preparation of the hormone-producing centers of the pancreatic tissue of healthy animals and that it accomplishes its results by acting as a substitute for the lacking pancreatic hormone of the diabetic's own blood.

The great importance of endocrine glands in controlling the later development of vertebrates, particularly the rôle they may play in determining the conformations of various parts of the body, opens up the important issue of how much such similarities are to be attributed to direct heredity, how much to endocrinal activities. Certain types of defectives such as cretins and so-called Mongoloids, even when of different races, often show marked resemblances (Fig. 30, p. 85). The abnormalities in the case of cretins are ascribed to endocrine—particularly to thyroid-deficiency in the affected individual, and those of Mongoloids are supposedly the result of endocrine disturbances in the mother or to fetal nutritive insufficiency. The Mongolian facial type, however, is also prevalent in cretins and may result from insufficiency of thyroid secretion during the growth period, since such lack is known to have a characteristic effect on the bones of the nose and the base of the skull. Thyroid as well as pituitary insuffi-

ciency may also be an important factor in dwarfing. From the standpoint of heredity, therefore, a peculiarity in a particular structure might have its immediate determining cause in the output of an endocrine gland, and if inheritance is involved, the determining genes would be those responsible for the changed condition of the gland in question, not for the visible, finished trait.

That all such developmental anomalies can not be attributed wholly to improper functioning of some endocrine gland of the affected individual, however, is shown by the fact that certain of them reveal their presence far back in the early fetus before its endocrine glands are functional. This is true, for example,



FIG. 30

Profiles of three Mongoloid imbeciles of two different racial stocks; left, Scotch; middle and right, Russian Jew. (After Davenport.)

of the achondroplastic dwarf, characterized by abnormally short and somewhat twisted arms and legs, with head and trunk of approximately normal size (Fig. 31, facing p. 86). Such individuals have many of the evidences—disproportionately broad face, low nose-bridge, overhanging forehead, undershot jaw—of thyroid deficiency. This abnormality, furthermore, can not be attributed, in all cases at least, to endocrinal defects of the mother, since pedigree tabulations are known which clearly show that the condition can be transmitted from the paternal side. Such a characteristic shaping-up of the head and face is due to lack of growth of the skull base. Professor Stockard points out the

resemblance of this condition in man to that found in certain breeds of the lower animals such as the bulldog and the pug-dog, and maintains that the underlying cause is probably the same in each. He believes, from our knowledge of their inheritance and development, that the primary cause lies in a germinal mutation or sport and that the endocrinal effects are secondary.

The English anatomist Keith is inclined to regard the primary differences which mark off the races of man as due to the relative activities of various endocrine glands. While his opinions are highly conjectural they are suggestive and show the importance of further investigation in this interesting field. Stature, for example, is largely regulated by the secretion from the pituitary gland, and Keith maintains that the average European is taller than the average negro or Mongolian because of the more pronounced activity of this gland in the Caucasian type. The pituitary also probably influences the character of the hair, the texture of the skin, and the cast of features. Hormones from the male gonad are apparently responsible for the main secondary sexual differences. Judging from the more heavily haired condition of the body in Caucasians, he likewise infers that this tissue is more active in them than in the Mongolian and negroid types. Again, he thinks that the lighter color of the paler-skinned races may have been produced by a greater activity of the adrenal glands since their secretion tends to destroy pigmentary bodies. According to his hypothesis, then, the Caucasian type is characterized by a relatively greater amount of internal secretion from gonads, and from pituitary, thyroid, and adrenal glands. Since racial characteristics are inherited, however, it is evident that such differences of mind or body, in so far as they are referable to the influence of internal secretions, must be assigned eventually to the germinal factors which determine the corresponding differences in the endocrinal glands.

Vitamines.—Before leaving the subject of remarkable reagents in the living organism which, although present in amounts almost infinitesimally small, are indispensable to the life processes, including growth and development, must be mentioned the vitamins. Discovered as recently as 1910, a great amount of information has already been obtained regarding them by the unremitting labor of investigators. Vitamines, as any one who reads the newspapers must know, are substances which are necessary, not only for our health and freedom from bodily



FIG. 31. Hindu dwarfs compared with normal Hindu (from *Treasury of Human Inheritance*). - From left to right: 1, cretin; 2 and 3, true dwarfs; 4 and 5, achondroplastic dwarfs; 6 normal Hindu.

malformations, but for life itself. Some four or five different kinds of vitamins have been identified and it seems not improbable that yet others may be discovered. Since attempts to isolate them in a pure state have failed, their appearance or chemical structure is wholly unknown. They can be extracted from certain foodstuffs in the form of solutions and we know their properties only by what happens in the nutrition, health or development of an individual when they are present in food or when they are not.

Vitamin "A" is abundant in butter, egg-yolk, cod-liver oil, and such leafy vegetables as green cabbage and spinach. It seems to be concerned with growth. Its absence is characterized by an eye-defect known as *xerophthalmia*. Vitamin "B" occurs in many vegetables and fruits, the germ of grains, and in milk, eggs and liver, but is deficient in most meats. Insufficient Vitamin "B" predisposes to the disease known as *beriberi*. Orange, lime and tomato juice are each rich in Vitamin "C," as are other fresh fruits and vegetables. Absence of "C" in food leads to the disease, *scurvy*. A Vitamin "E," occurring abundantly in wheat germs, has been found to favor fertility and lactation in mammals.

A remarkable relation between Vitamin "D" (the "anti-rachitic" vitamin) and light rays has recently been disclosed by Steenbock, through the irradiation of various substances with ultra-violet rays or through exposure to direct sunlight. Cod-liver oil is naturally rich in this vitamin. By exposing thin films of olive oil, lard or other oils to direct sunlight or to ultra-violet light, they, too, become rich in Vitamin "D." Lack of "D," apparently by interfering with calcium metabolism, results in insufficient calcium in the bones and other tissues, and thus leads to suspension of proper growth and the occurrence of the deficiency disease known as *rickets*.

Conclusions Regarding the Mechanics of Development.—As to what we are to conclude about the mechanics of development from such facts as have been reviewed, the complete answer is by no means evident. It seems probable that in most eggs, under normal conditions of development, a given part does have a prospective relation to specific parts of the developed organism, but in many cases this prospective outcome is not unalterable. It is prospective only in the sense that in the original normal egg it constitutes part of a particular internal

organization which, subject to the operation of certain external factors termed the normal environment, will give rise to a developed individual.

In regeneration or regulation, whether it be merely restoration of a lost appendage, or the development of a complete body from a fragment of an old one, the phenomenon is obviously of one piece with the more ordinary phenomenon of development. For whether the case be one of development from the egg, of budding or fission, or of restitution, the problem is that of explaining the genesis of distinctive organs and attributes from a fundamental protoplasmic mass of definite and specific constitution and ancestry. The fact must not be lost sight of that when, for instance, a new head with tentacles is caused to develop on the side of *Cerianthus*, it is a *Cerianthus* head, not that of some other form. Likewise, although the prawn may develop an antenna in place of a removed eye, nevertheless it is an antenna still characteristic of the crustacean organism which bears it. And so for the other examples reviewed. No matter how marked an effect may result from the modifications of external conditions, the quality of the reaction is in the main always determined by the nature of the organism. While external agents may be of great importance as stimulus, and while unquestionably environment restricts or conditions and sometimes markedly modifies the outcome, the nature of the response is determined by the inherited organization of the developing form. Specific forms, then, though they may be greatly modified by external conditions, are not *caused* by them.

Within the organism itself, however, we have seen that the same initial materials may yield very different end-products under different conditions. Blastomeres originally directed toward becoming one part of an individual may be switched about to become another part; tissues originally subserving one function may be turned to other uses; fragments of the simpler animals may remodel themselves into complete individuals of smaller size. The production of double monsters, of identical twins or of several individuals from one original oöperm, as in the armadillo (Fig. 32, p. 89), indeed, all point to the same conclusion. The inescapable inference is, in brief, that a particular cell takes on the characteristics of a special tissue, not because it differs constitutionally from other cells, but because of the differential nature of the stimuli to which earlier it has been exposed or

to which it is subjected as a result of its special location in the developing organism; that all the descendants of the fertilized ovum, germinal and somatic cells alike, retain the hereditary potencies of the original zygote. Because of limitations due to its particular location in the organism, however, a given cell realizes only a small proportion of its inherent possibilities.

Since, then, the distinctive structural effects and functions which characterize the respective tissues are probably the outcome of unlike activities among the same kinds of fundamental protoplasmic constituents in differing local environments, the "germ-plasm," recognized so universally by biologists as the



FIG. 32

Four young armadillos all from the same fetal envelope (after Newman and Patterson). All four originally from the same egg, hence all are of the same sex and otherwise very similar.

actual substance of inheritance, must be something that is present in every cell. While, obviously, all cells have it, ordinarily only the cells specialized as reproductive cells pass it on in the form of a new generation. This "something" we shall find in subsequent chapters, is in all probability the chromosomes of the cell-nucleus.

A theory propounded by Holmes some years ago perhaps accounts for the known facts of form regulation in organisms

as satisfactorily as any yet proposed. Holmes believes that each part of an organism derives certain advantages, in the form of substance or stimuli, from its neighboring parts, and that these in turn receive advantages from it. Unspecialized cells produced in the place of a removed part have pressure put upon them to specialize in the direction of the cells which made up the missing part because this would secure the advantages afforded by the original interdependent relationship. The same principle of mutual dependence would apply in embryonic development. Holmes illustrates by pointing out an analogy in human society thus:

"If all bricklayers should suddenly disappear, their ranks would soon be filled by other people who would respond to the increased demand that would be created for this particular kind of workers. The similarities in the processes of regeneration and adjustment that go on in the individual and in the social group represent something more than mere analogy. Both societies and individual organisms are composed of units which tend to grow and perpetuate their kind. The units of both have a considerable degree of plasticity, especially in early stages, and what each unit may become is largely determined in accordance with the principle of supply and demand as well in the individual organism as in human industrial society."

CHAPTER VI

THE BEARERS OF THE HERITAGE

The Origin of the New Germ-Cells.—On account of the unusual importance from the standpoint of inheritance, which attaches to the germ-cells, more must be said about their origin and behavior. While the evidence is conflicting in many cases, in some it has been well established that the germ-cells are set apart very early from the cells which are to differentiate into the ordinary body tissues. Fig. 33*A*, p. 92, shows a section through the eight-celled stage of *Miastor*, a fly, in which a single large, primordial germ-cell (*p. g. c.*) has already been set apart at one end of the developing embryo. The nuclei of the rest of the embryo still lie in a continuous protoplasmic mass which has not yet divided up into separate cells. The densely stained nuclei at the opposite end of the section are the remnants of nurse-cells which originally nourished the egg. Fig. 33*B*, p. 92, is a longitudinal section through a later stage in the development of *Miastor*; the primitive germ-cells (oög) are plainly visible. Still other striking examples might be cited. Even in vertebrates the germ-cells may often be detected at a very early period, although their exact origin is a matter in dispute.

Germinal Continuity.—The germinal substance which is to carry on the race is thus ordinarily set aside at an early period in the individual; it takes no part in the formation of that individual's body, but remains a slumbering mass of potentialities which must bide its time to awaken into expression in a subsequent generation. The egg, in other words, does not develop into a body which in turn makes new germ-cells, but body and germ-cells are established at the same time, the body harboring and nourishing the germ-cells, but not generating them (Fig. 2, p. 11). This need not necessarily mean that the germ-cells have remained wholly unmodified or that they continue uninfluenced by the conditions which prevail in the body, especially in the nutritive blood and lymph stream, although as a matter of fact most biologists are extremely skeptical as to the probability that

influences from the body, beyond such general indefinite effects as might result from under-nutrition or from poisons carried in the blood, modify the intrinsic nature of the germinal substances to any measurable extent.

The fact should not be overlooked, however, that somatic cells and germ-cells alike are descendants of the original fertilized ovum and that all, therefore, possess its properties. In plants and in the less highly specialized animals, as a matter of fact, ordinary tissue-cells may take on germinal functions; and the phenomena of regeneration and reconstitution demonstrate the same basic capacity. This is understandable in the light of the

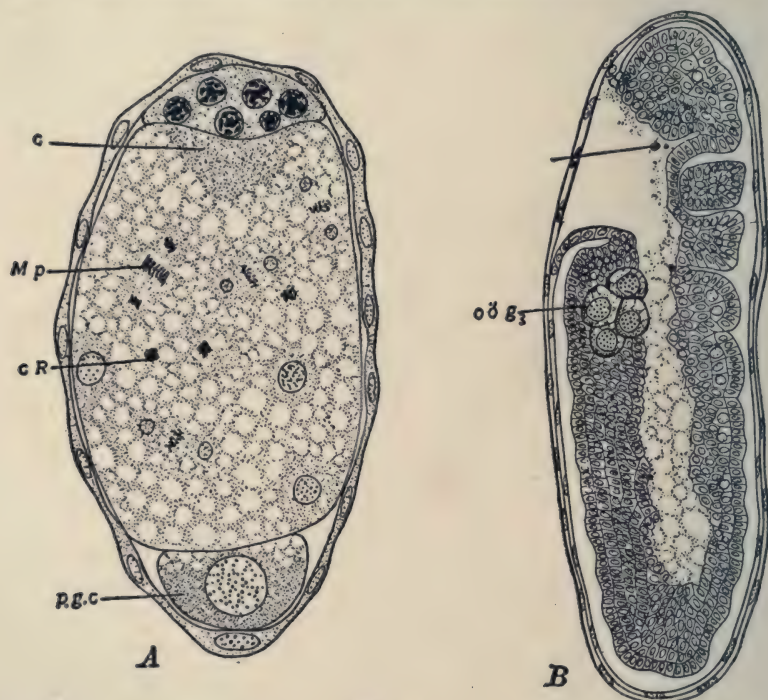


FIG. 33

A—Germ-cell (*p, g, c*) set apart in the eight-celled stage of cleavage in *Miastor americana* (after Hegner). The walls of the remaining seven somatic cells have not yet formed though the resting or the dividing (*M p*) nuclei may be seen; *c R*, chromatin fragments cast off from the somatic cells.

B—Section lengthwise of a later embryo of *Miastor*; the primordial egg-cells (*oö g₁*) are conspicuous (after Hegner).

community of origin of all cells. The differences between germ-cells and tissue-cells, indeed, are probably not differences in fundamental constitution but, as shown by the facts of developmental mechanics (Chapter V), differences in specialization. Thus while the representative leaven necessary for the establishment of a new individual is common to all cells, in higher animals the germ-cell alone is the living bond between generations. A substance which fulfills the requirements of such *germinal continuity*, whether it be from cell to cell in the developing individual or by way of the germ-cells to the new generation, is found, as we shall see immediately, in the chromosomes of the nucleus.

When the organism is ready to reproduce its kind the germ-cells awaken to activity, usually undergoing a period of multiplication to form more germ-cells before finally passing through a process known as *maturation*, which makes them ready for fertilization. The maturation process proper, which consists typically of two rapidly succeeding divisions, is preceded by a marked growth in size of the individual cells.

Individuality of Chromosomes.—Before we can understand fully the significance of the changes which go on during maturation we shall have to know more about the conditions which prevail among the chromosomes of cells.

As already noted each kind of animal or plant has its own characteristic number and types of chromosomes when these appear for division by mitosis. In many organisms the chromosomes are so nearly of one size as to make it difficult or impossible to be sure of



FIG. 34

A. Chromosomes of the mosquito (*Culex*) after Stevens.

B. Chromosomes of the squash bug (*Anasa tristis*) after Wilson.

the identity of each individual chromosome, but on the other hand, there are some organisms known in which the chromosomes of a single nucleus are not of the same size and form (Fig. 34, above). These latter cases enable us to determine some very significant facts. Where such differences of shape and proportion occur they are constant in each succeeding division so that similar chromosomes may be identified each time. Moreover, in all ordinary mitotic divisions where the conditions are accurately known, these chromosomes of different types are found to be present as pairs of similar elements; that is, there are—with

minor exceptions which but add to the significance of the facts—two of each form or size.

Pairs of Similar Chromosomes in the Nucleus Because One Chromosome Comes from Each Parent.—When we recall that the original fertilized egg from which the individual develops is really formed by the union of two gametes, ovum and spermatozoon, and that each gamete, being a true cell, must carry its own set of chromosomes, the significance of the pairs of similar chromosomes becomes evident; one of each kind has been contributed by each gamete. This means that the zygote or fertile ovum contains double the number of chromosomes possessed by either gamete, and that, moreover, each tissue-cell of the new individual will contain this dual number. For, as we have seen, the number of chromosomes is, with possibly a few exceptions, constant in the tissue-cells and early germ-cells in successive generations of individuals. For this to be true it is obvious that in some way the nuclei of the conjugating gametes have come to contain only half the usual number. Technically the tissue-cells are said to contain the *diploid* number of chromosomes, the gametes the reduced or *haploid* number.

In Maturation the Number of Chromosomes is Reduced by One-Half.—This halving, or as it is known, *reduction* in the number of chromosomes is the essential feature of the process of maturation. It is accomplished by a modification in the mitotic division in which instead of each chromosome splitting lengthwise, as in ordinary mitosis, the chromosomes unite in pairs (Fig. 35*b*, p. 95), a process known technically as *synapsis*, and then apparently one member of each pair passes entire into one new daughter-cell, the other member going to the other daughter-cell (Fig. 35*c*, p. 95). In the pairing preliminary to this *reduction division*, leaving out of account certain special cases to be considered later, according to the best evidence at our command the union always takes place between two chromosomes which match each other in size and appearance. Since one of these is believed to be of maternal and the other of paternal origin, the ensuing division separates corresponding mates and insures that each gamete gets one of each kind of chromosome although it appears to be a matter of mere chance whether or not a given cell gets the paternal or the maternal representative of that kind.

Maturation of the Sperm-Cell.—In the maturation of the male gamete the germ-cell, known as a *spermatogonium*, increases

greatly in size to become a *primary spermatocyte*. In each primary spermatocyte the pairing of the chromosomes already alluded to occurs as indicated in Fig. 35*b*, below, where six is taken arbitrarily to indicate the ordinary or *diploid* number of chromosomes, and three the reduced or *haploid* number. The division of the primary spermatocyte gives rise to two *secondary spermatocytes* (*c*), the paired chromosomes separating in such a way

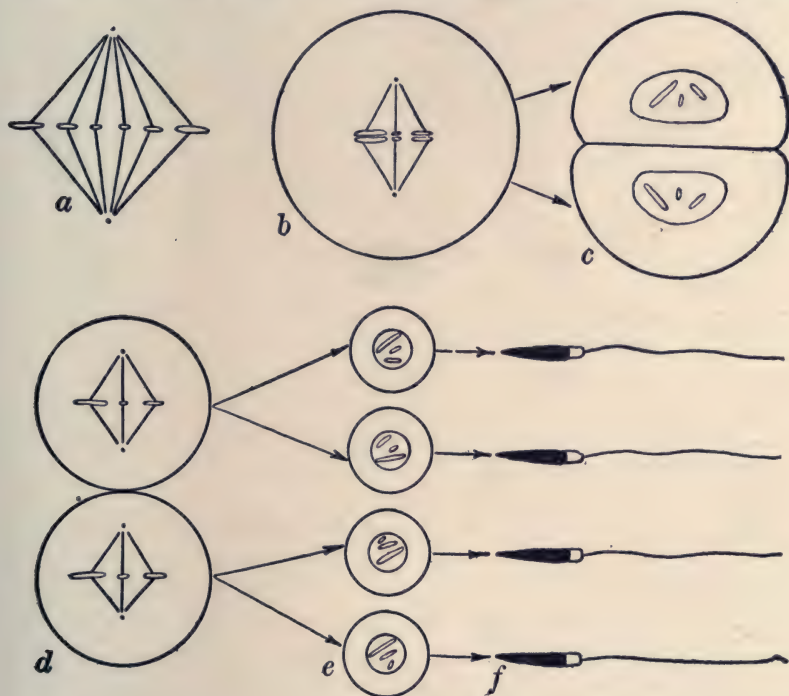


FIG. 35

Diagram to illustrate spermatogenesis: *a*, showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in divisions of ordinary cells and spermatogonia; *b*, the pairing (synapsis) of corresponding mates in the primary spermatocyte preparatory to reduction; *c*, each secondary spermatocyte receives three, the haploid number of chromosomes; *d*, division of the secondary spermatocytes to form *e*, spermatids, which transform into *f*, spermatozoa.

that a member of each pair goes to each secondary spermatocyte. Each secondary spermatocyte (*d*) soon divides again into two *spermatids* (*e*), but in this second division the chromosomes

each split lengthwise as in an ordinary division so that there is no further reduction. In some forms the reduction division occurs in the secondary spermatocytes instead of the primary. Each spermatid transforms into a mature *spermatozoon* (*f*) although in so doing it is not uncommon for much of the cytoplasm to be discarded. The spermatozoa of most animals are of linear form, each with a head, a middle piece and a long vibratile tail which is used for locomotion. The head consists for the most part of the transformed nucleus and is consequently the part which bears the chromosomes.

Maturation of the Egg-Cell.—As regards the behavior of the chromosomes the maturation of the ovum parallels that of the sperm-cell. There are not so many primordial germ-cells formed and only one out of four of the ultimate cells becomes a functional egg. As in maturation of the sperm-cell there is a growth period in which *oögonia* enlarge to become primary oöcytes (Fig. 36*b*, p. 97). In each primary oöcyte as in the primary spermatocyte the chromosomes pair and two divisions follow in one of which the typical numerical reduction in the chromosomes occurs. A peculiarity in the maturation of the ovum is that there is a very unequal division of the cytoplasm in cell division so that three of the resulting cells usually termed *polar bodies* are very small and appear like minute buds on the side of the fourth or egg-cell proper.

The scheme of this formation of the polar bodies is indicated in Fig. 36, p. 97. In Fig. 36*b* the chromosomes are seen paired and ready for the first division; that is, for the formation of the first polar body. Figs. 36*c*, *d*, show the giving off of this body. Note that while only a small proportion of the cytoplasm passes into this tiny cell, its chromatin content is as great as that of the ovum. A second polar body (Figs. 36*e*, *f*) is formed by the egg, but in this case each chromosome splits lengthwise, as in ordinary mitosis, and there is no further numerical reduction. In the meantime, typically, a third polar body is formed by division of the first (stages *e*, *f*, *g*).

Parallel between the Maturation of Sperm- and Egg-Cell.—This rather complex procedure of the germ-cells will be rendered more intelligible through a careful study of Figs. 35 and 36, pp. 95 and 97, and Fig. 37, p. 98, which indicates the parallel conditions in spermatogenesis and oögenesis.

The view now generally held regarding the polar bodies is that

they are really abortive eggs. They later disappear, taking no part in embryo formation. It can readily be seen how such an unequal division is advantageous to the large cell, for it receives all of the rich store of food material that would be distributed among the four cells if all were of equal size. This increased amount of food is a favorable provision for the forthcoming offspring whose nourishment is thus more thoroughly insured.

On the other hand, all of the sperm-cells develop into complete active forms, which, as aforesaid, usually become very

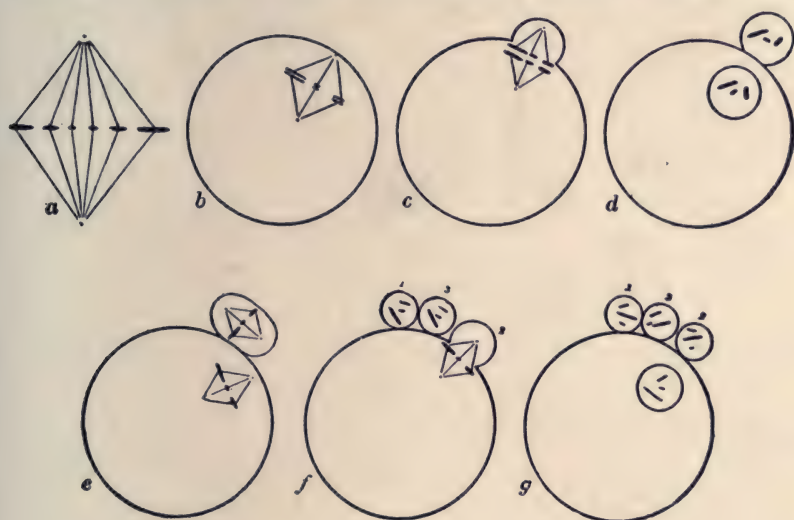


FIG. 36

Diagram to illustrate oögenesis: *a*, showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in ordinary cells and oögonia; *b*, the pairing of corresponding mates preparatory to reduction; *c*, *d*, reduction division, giving off of first polar body; *e*, egg preparing to give off second polar body, first polar body ready for division; *f*, *g*, second polar body given off, division of first polar body completed. The egg nucleus, now known as the female pronucleus, and each body contain the reduced or haploid number of chromosomes.

much elongated and develop a motile organ of some kind. In such cells an accumulation of food to any large extent would hinder rather than help them, because it would seriously interfere with their activity.

Fertilization.—In fertilization (Fig. 38, p. 100), the spermatozoon penetrates the wall of the ovum and after undergoing

considerable alteration its nucleus fuses with the nucleus of the egg. In some forms only the head (nucleus) and middle piece, or rarely even the head alone, enter, but in most cases the whole spermatozoon passes in although the tail seems to take no part

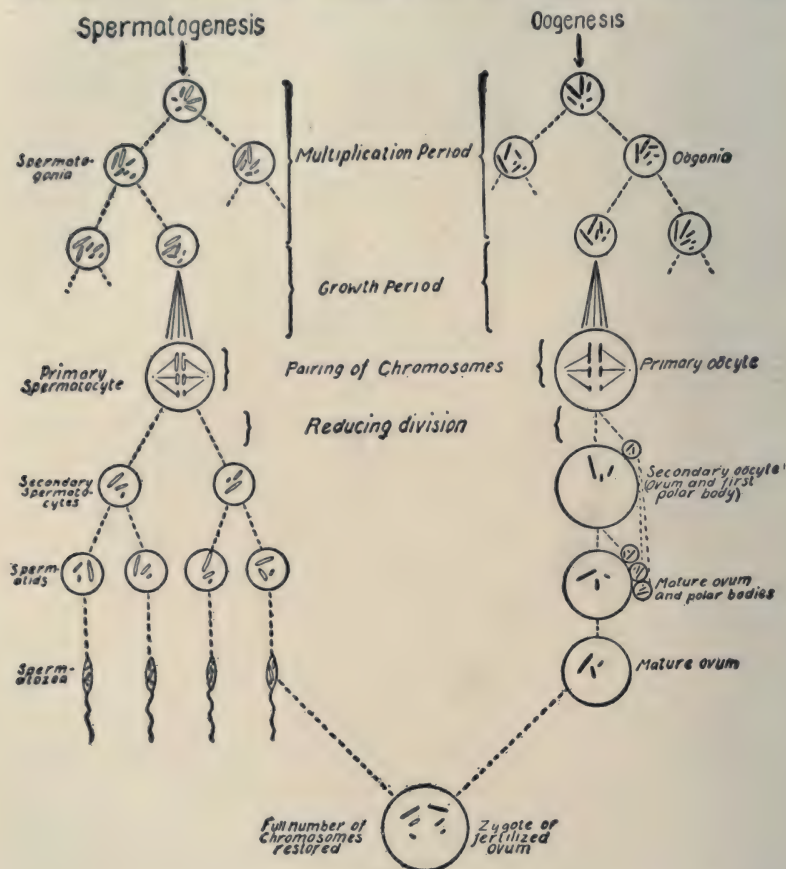


FIG. 37

Diagram showing the parallel between maturation of the sperm-cell and maturation of the ovum.

in subsequent events. Immediately following entrance of the sperm a so-called *fertilization membrane* becomes visible over the surface of the egg. Normally only one spermatozoon unites with an egg. In some forms while several may enter only one

becomes functional. As soon as the nucleus of the spermatozoon, now known as the male *pronucleus*, reaches the interior of the egg, it enlarges and becomes similar in appearance to the female *pronucleus*. It swings around in such a way (Fig. 38*b*) that the middle piece, now transformed into a centrosome, lies between it and the female pronucleus. The two pronuclei (*c*, *d*, *e*), each containing the reduced number of chromosomes, approach, the centrosome divides, the nuclear walls disappear, the typical division spindle forms, and the chromosomes of paternal and maternal origin respectively come to lie side by side at the equator of the spindle ready for the first division of cleavage (*f*, *g*). It will be noted that the individual chromosomes do not intermingle their substance at this time, but that each apparently retains its own individuality. There is considerable evidence, particularly in the cells of certain hybrids from parents with unlike chromosomes, which indicates that throughout life the chromosomes contributed by the male remain distinct from those of the female parent. Inasmuch as each germ-cell, after maturation, contains only half the characteristic number of chromosomes, the original number is restored in fertilization.

Significance of the Behavior of the Chromosomes.—The question confronts us as to what is the significance of this elaborate system which keeps the chromosomes of constant size, shape and number; which partitions them so accurately in ordinary cell divisions; and which provides for a reduction of their numbers by half in the germ-cell while yet securing that each mature gamete gets one of each kind of chromosome. Most biologists look on these facts as indicating that the chromosomes are specifically concerned in inheritance.

In the first place it is recognized that as regards the definable characters which separate individuals of the same species, offspring may inherit equally from either parent. And it is a very significant fact that while the ovum and spermatozoon are very unequal in size themselves, the chromosomes of the two germ-cells are of the same size and number. The human ovum, for example, although itself only about $1/125$ of an inch in diameter, has a volume about thirty-five thousand times that of the sperm. The parity in chromosomal contribution points clearly to the means by which an equal number of character-determiners might be conveyed from each parent. Moreover it is mainly the nucleus of the sperm-cell in some organisms which enters the egg, hence

the determiners from the male line must exist wholly or largely somewhere in the nucleus. And the bulk of the nucleus in the spermatozoon consists of the chromosomes or their products.

Boveri, furthermore, by causing cleavage irregularities, has

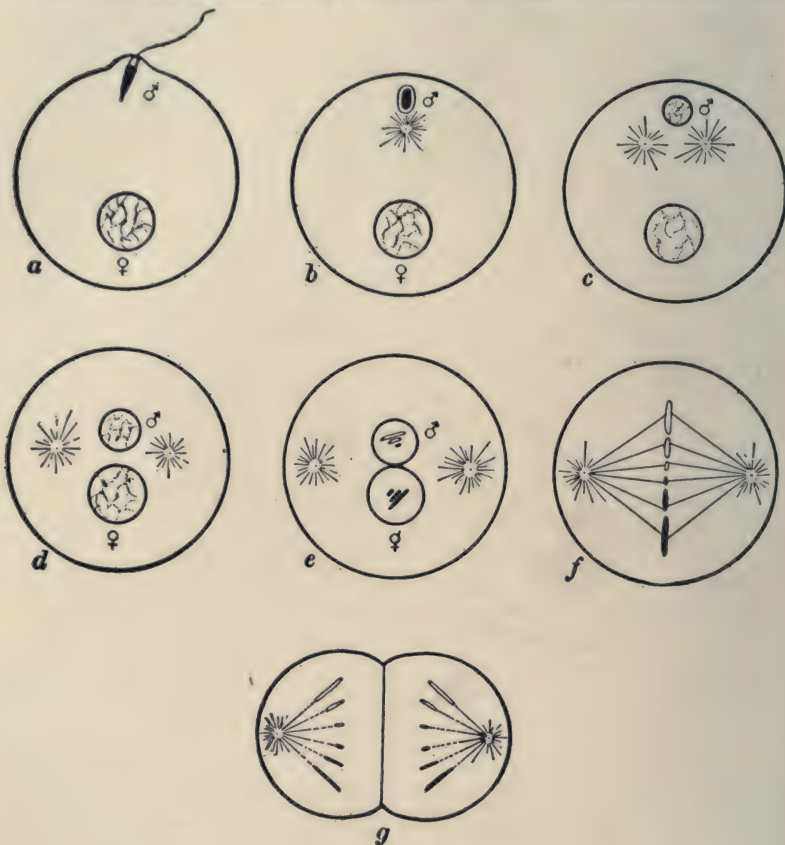


FIG. 38

Diagram to illustrate fertilization; ♂, male pronucleus; ♀, female pronucleus; observe that the chromosomes of maternal and paternal origin respectively do not fuse.

shown experimentally that in sea-urchins normal development requires normal chromosome combination or, in other words, that each chromosome plays a different part in the development of the individual and therefore in determining heredity. And

Bridges found in the fruit fly (*Drosophila*), a correlation between the presence and absence of certain characters and the presence or absence of a particular chromosome. Lastly, the facts of genetics, to be reviewed later, require for their explanation just such a material basis as the chromosomes appear to be.

A Single Set of Chromosomes Derived from One Parent Only is Sufficient for the Production of a Complete Organism.

—That a single or haploid set of chromosomes as seen in the gametes is sufficient contribution of chromatin for the production of a complete organism is proved by the fact that the unfertilized eggs of various animals (many echinoderms, worms, mollusks, and even the frog) may be artificially stimulated to development without uniting at all with a spermatozoon. The resulting individual is normal in every respect except that instead of the usual diploid number it has only the single or haploid number of chromosomes. Its inheritance of course is wholly of maternal origin. The converse experiment in echinoderms in which a nucleus of male origin (that is, a spermatozoon) has been introduced into an egg from which the original nucleus has been removed shows that the single set of chromosomes carried by the male gamete is also sufficient to cooperate with the egg-cytoplasm in developing a complete individual.

In the honey-bee the males or drones come from unfertilized eggs. As a consequence the cells of their tissues, including the germ-cells, have only the haploid number of chromosomes. The workers and queens on the other hand come from fertilized eggs and display the diploid number of chromosomes. Since the males already have the reduced number of chromosomes no further reduction occurs. The first spermatocyte division is abortive; all the chromosomes remain in one cell and only a minute cytoplasmic globule, representing the other cell, is budded off.

The Duality of the Body and the Singleness of the Germ.—Since every chromosome of maternal origin in the ordinary cell has an equivalent mate derived from the male parent, it follows therefore, supposing the chromosomes do have the significance in inheritance attributed to them, that as regards the measurable inheritable differences between two individuals, the ordinary organism produced through the union of the two germ-cells is, potentially at least, dual in nature. On the other hand through the process of reduction the gametes are provided with only a single set of such representatives. This duality of the body and

singleness of the mature germ is one of the most striking facts that come to light in embryology. How well the facts fit in with the behavior of certain hereditary characters will be seen later in our discussions of Mendelism.

The Cytoplasm Not Negligible in Inheritance.—Just what part is played by the cytoplasm in inheritance is not clear, but it is probably by no means a negligible one. The cytoplasm of a given organism is just as distinctive of the species or of the individual of which it forms a part as are the chromosomes. It is well established that neither nucleus nor cytoplasm can fully function or even exist long without the other, and neither can alone produce the other. They undoubtedly must cooperate in building up the new individual, and the cytoplasm of the new individual is predominantly of maternal origin. It is obvious that all of the more fundamental characters which make up an organism, such, for instance, as make it an animal of a certain order or family, as a human being or a dog or a horse, are common to both parents, and there is no way of measuring how much of this fundamental constitution comes from either parent, since only closely related forms will interbreed. In some forms, moreover, the broader fundamental features of embryogeny are already established before the entrance of the spermatozoon. We may infer that in the development of the new being the chromosomes of the egg together with those derived from the male work jointly on or with the other germinal contents which are mostly cytoplasmic materials of maternal origin. Clearly the cytoplasm must be of a nature to respond specifically when thus acted upon.

The Chromosomes Responsible for the Distinctiveness of Given Characters.—It seems probable that in the establishment of certain basic features of the organism the cooperation of the cytoplasm with chromatin of either maternal or paternal origin might accomplish the same end, but that certain distinctive touches are added or come cumulatively into expression through influences carried, predominantly at least, in the chromatin from one as against the other parent. These last distinctive characters of the plant or animal constitute the individual differences of such organisms. In this connection it is a significant fact that in young hybrids between two distinct species the early stages of development, especially as regards symmetry and regional specifications, are exclusively or predominantly maternal in character,

but the male influence becomes more and more apparent as development progresses until the final degree of intermediacy is attained.

From the evidence at hand this much seems sure, that the paternal and maternal chromosomes respectively carry substances, be they ferments, nutritive materials or what not, that are instrumental in giving the final parity of personal characters which we observe to be equally heritable from either line of ancestry. It is clear that most of the characters of an adult organism can not be merely the outcome of any unitary substance of the germ. Each is the product of many cooperating factors and for the final outcome any one cooperant is probably just as important in its way as any other. The individual characters which we juggle to and fro in our breeding experiments seem apexed, as it were, on more fundamental features of organic chemical constitution, polarity, regional differentiation, and physiological balance, but since such individual characters parallel so closely the visible segregations and associations which go on among the chromosomes of the germ-cells it would seem that they, at least, are represented in the chromosomes by distinctive cooperants which give the final touch of specificity to those hereditary characters which can be shifted about as units of inheritance.

Sex and Heredity.—Whatever the origin of fertilization may have been in the world of life, or whatever its earliest significance, the important fact remains that to-day it is unquestionably of very great significance in relation to the phenomena of heredity. For in all higher animals, at least, offspring may possess some of the characteristics originally present in either of two lines of ancestry, and this commingling of such possessions is possible only through sexual reproduction. As has already been seen, in the pairing of chromosomes previous to reduction, the corresponding members (*homologous chromosomes*) of a pair always come together so that in the final segregation each gamete is sure to have one of each kind although whether a given chromosome of the haploid set is of maternal or paternal origin seems to be merely a matter of chance. Such random assortment, indeed, has been actually observed by Carothers and others in the germ-cells of various species of grasshoppers in which the two chromosomes that pair are sufficiently unlike to permit of identification. Thus, for instance, if we arbitrarily represent the chromosomes of a given individual by *ABC abc*, and regard *A*, *B* and *C* as of

paternal and a , b and c as of maternal origin, then in synapsis only A and a can pair together, B and b , and C and c , but each pair operates independently of the other so that in the ensuing reduction division either member of a pair may get into a cell with either member of the other pairs. That is, the line for division at a given reduction might be any one of the following, $\frac{A B C}{a b c}$, $\frac{A B c}{a b C}$, $\frac{A b c}{a B c}$, $\frac{A b C}{a B C}$. This would yield the following eight kinds of gametes, ABC , abc , ABc , abC , Abc , aBC , AbC , aBc , each bearing one of each kind of chromosome required to cover the entire field of characters necessary to a complete organism. And since each sex would be equally likely to have these eight types of gametes and any one of the eight in one individual might meet any one of the eight of the other, the possible number of combinations in the production of a new individual from such germ-cells would 8×8 , or 64.

While there are 64 possible combinations where each gamete in one sex is exactly duplicated in the other, a tabulation of these (compare table on p. 145) would show that, because of repetitions, only 27 are *different* combinations. The following simple formulæ are useful in computing such combinations: where n represents the number of pairs of chromosomes in the individual, 2^n indicates the number of different gametes in each sex; $(2^n)^2$, the number of possible combinations, and 3^n the number of different combinations producible, when, as in self-fertilizing plants, for instance, the sets of chromosomes in the gametes of one sex are exactly duplicated in the other sex. In the foregoing example then, where three pairs of chromosomes were involved: $n = 3$; $2^n = 2^3 = 8$; $(2^n)^2 = (2^3)^2 = 64$; and $3^n = 3^3 = 27$.

In matings between unrelated forms, however, where presumably the individual chromosomes in the gametes of the male sex are not exact duplicates of those of the female the number of *possible* combinations would also represent the number of *different* combinations, as there would be no repetitions due to identical chromosomes in the two sexes. In other words $(2^n)^2$ would represent the number of different combinations. In man where there are twenty-four pairs of chromosomes, computation on this basis shows the number of different combinations producible, $(2^{24})^2$, to be 1,125,789,906,742,624.

As a matter of fact modern man is passing to and fro in genetic relations the same fundamental forty-eight chromosomes which

characterized the human species at its dawn. The innumerable hereditary differences which exist between races or individuals must, therefore, be the result of constitutional changes which have taken place in the substance of the various chromosomes themselves. It is obvious that once such a constitutional change occurs in any chromosome, as a result of sexual reproduction it eventually becomes instilled into the race or stock. Constant novelty is thus being introduced and spread through chromosome recombinations generation after generation, thereby making for greater diversity in offspring. It is probable, however, that, in a closely related stock at least, much of the substance of any particular chromosome in an individual is a duplicate of that of the corresponding chromosome in a fellow individual. The differences which creep in from time to time apparently represent restricted regions rather than the entire chromosome. It is not improbable, indeed, that the fundamental constitution of each of the 24 kinds of chromosomes in man is similar in many respects in all human beings.

CHAPTER VII

SEX AND THE SEX-CHROMOSOMES

The Wide Occurrence of Sex Argues Its Importance.—Regarding the full significance of sex, there is no unanimity of opinion. That cross-fertilization is advantageous has been established in many cases, notably in many plants where this is evidenced by increased vigor and productivity, but just wherein lies the advantage is not so well understood. On the other hand there are many plants and some animals known which are self-fertilizing yet these seem to be as successful as any in the struggle of life. However, in nearly all such forms it is probable that cross-fertilization occurs from time to time. In most animals which bear both ova and sperm in the same individuals (*hermaphrodites*), special means are provided to prevent self-fertilization.

The occurrence of sex throughout the whole gamut of life from protozoa to man is a self-evident expression of its importance. It so pervades the make-up of most animals, especially higher forms, that the significance of much of their structure and behavior is interpretable only in terms of sex. For not only have structures arisen connected directly with the reproductive system but a multitude of secondary characters such as ornaments, regarded by some as for sexual allurements, weapons such as antlers or spurs for combat, and many special features of behavior have appeared. It is a trite observation that many of the frills and furbelows of human life hark back primarily to the sex instinct and much of its drama revolves about the facts of sex.

Two Functions Performed by Normal Fertilization.—It has become apparent from many investigations, however, that fertilization is by no means identical with reproduction. Fertilization, as it ordinarily occurs, performs two distinct functions that may be separated experimentally. On the one hand it initiates development in an egg and on the other it brings about inheritance from two parents. The first function can be replaced in numerous forms by artificial means such as subjection of the egg to tem-

perature changes, osmotic changes, certain chemicals, or even to mild shaking or the prick of a needle. But in such cases of *artificial parthenogenesis*, as in natural parthenogenesis, the offspring has only one line of ancestry back of it.

The Theory of Rejuvenescence.—As with many of their problems biologists have sought to discover the significance of sex by studying it in the lower animals where it stands revealed in its least complex form. Inasmuch as well developed sexual conditions exist even in the protozoa, the animals of this group have been particularly studied. It has already been seen how the unicellular forms reproduce through self-division. Reproduction by this method goes on for a number of generations, possibly a few hundred, when, under the ordinary conditions of life in most protozoa, such periods of multiplication are interrupted by the union or *conjugation* of individuals in pairs. Two individuals may fuse completely into one, as in certain amebæ or in various flagellate forms. In other cases, as in *Paramecium*, a ciliated form, the union is only temporary but while together the two individuals exchange part of their nuclear material. Through such conjugation, according to the views of some biologists, a *rejuvenescence* has been accomplished which renews the vigor of the conjugating individuals and thus prevents deterioration.

Some have maintained that protoplasm, whether in unicellular or multicellular organisms, after continued physiological activity becomes senescent, possibly through the accumulation of metabolic products, and that it is rejuvenated by the stirring up it undergoes through the fusion of two masses of living substance slightly dissimilar in constitution. Others have suggested that one of the chief characteristics of living matter is its ceaseless mobility, its continual waste and repair and shifting equilibrium, and that after a time it tends to become more and more stable. But stable protoplasm means dead protoplasm, hence the vital substance of the living organism must undergo more or less of an upheaval from time to time, and this is normally accomplished through the mixtures of the plasmas of two different organisms.

Doubt, however, has been thrown upon the theory of rejuvenescence—or at least upon the view that fertilization is indispensable to the perpetuation of living matter—not only by the fact that many plants seem able to reproduce interminably by asexual methods, but because among the protozoa themselves non-conjugating strains have been discovered.

Professor Woodruff has isolated strains of *Paramecium*, for example, which under favorable environmental conditions can reproduce indefinitely without conjugation. After fourteen years and over ten thousand generations, in carefully controlled cultures where conjugation was impossible, the individuals were still normally active and without sign of degeneration.

In such forms as *Paramecium*, however, a process of internal nuclear reorganization known as *endomixis* occurs periodically even in non-conjugating forms which apparently effects a physiological stimulation similar to that which follows conjugation. This suggests that some form of occasional stimulus to protoplasmic activity is necessary and that the usual means of insuring it is through fertilization but that under special conditions this method is replaced by some other.

Professor Calkins has shown conclusively that in the ciliate *Uroleptus* actual rejuvenescence follows conjugation. In this species, after some two hundred or more divisions, in the absence of conjugation the division rate slows down and the individuals pass into a decline followed by structural degeneration and death. Conjugation, however, renews the waning metabolic activities of the cell and initiates a new cycle of active growth and division.

Biparental Inheritance Produces Variety in Protozoa.—Professor Jennings carried on observations for a number of years to get at the actual effects of conjugation in certain protozoa. He made exhaustive studies to determine in what respects, other conditions being the same, conjugating and non-conjugating members of the same stock or of different stocks differ. One of his fundamental experiments was to divide a given strain into two parts and keep them under identical conditions except that conjugation was permitted in the one line and prevented in the other.

In the inter-change of nuclear material between the two conjugating individuals if, as we have every reason to believe, such materials have to do with the determination of hereditary characters, then it is obvious that new combinations of such materials must occur and that therefore the progeny will differ from the parents, or in other words conjugation brings about great variety. This, according to Jennings, seems to be its chief significance. Where under the prevailing conditions the existing combinations are not adapted to survival, as

evidenced by the dying out of the race, conjugation of such perishing individuals results in the production of many new combinations, some of which are adapted to the situation. It is a significant fact that unfavorable changes of the conditions under which such infusoria live usually induce conjugation. The general relation between sex and heredity in the higher animals has already been discussed (p. 103).

Non-Sexual Rejuvenescence.—The views of Child on rejuvenation have already been reviewed (p. 77). While apparently sexual reproduction does not occur in certain flatworms a rejuvenation is nevertheless accomplished, he thinks, through the reproductive fragmentation of the body of the senescent individual. Each fragment forms a case or *cyst* around itself, and becomes reconstituted into a small, whole, physiologically young animal. Child finds that senescence is associated with growth in this form and that such an asexual reproduction as that described results from the accompanying slowing down of the rate of metabolism. Reconstitution of artificially isolated pieces of many of the lower organisms occurs and Child considers these likewise as cases of rejuvenescence. He regards senescence as due to a decrease in the rate of metabolism which results from the accumulation of obstacles incident to growth and differentiation, and he looks upon rejuvenescence as an increase in the metabolic rate resulting from the removal of relatively inactive substances, or from other changes which permit an increase in the rate of reaction. Since egg-cell and spermatozoon are highly specialized, he considers them old and believes that fertilization initiates a process of rejuvenescence in them.

Accepting a theory of rejuvenescence does not invalidate in any way, of course, the conception that the two fusing germ-cells also mingle two lines of hereditary characteristics and therefore produce great variety.

Many Theories of Sex Determination.—From earliest times the problem of sex determination has been one of keen interest, and needless to say hundreds of theories have been propounded to explain it. Geddes and Thomson say that Drelincourt recorded two hundred sixty-two so-called theories of sex production and remark that since his time the number has at least been doubled. The desirability of controlling sex has naturally appealed strongly to breeders of domesticated animals.

A study of animals born in litters, or twins, is enough in

itself to make us skeptical of theories of sex determination based on nutritional or external factors. In a litter of puppies, for example, there are usually both males and females, although in their prenatal existence they have all been subject to the same nutritional and environmental conditions. Likewise in ordinary human twins one may be a boy, the other a girl, whereas if the nutritional condition of the mother were the fact determining sex, both should be boys or both girls. However, there are twins known as *identical twins* who are remarkably alike and who are always of the same sex. But there is reason to suppose that identical twins in reality come from a single zygote which divides at an early period into two separate embryos. Such twins are monochorial; that is, they grow inside the same fetal membrane, whereas each ordinary twin has its own fetal membrane and has obviously originated from a separate ovum. In man, ordinary twins are no more alike than ordinary brothers and sisters, but identical twins are strikingly similar in structure, appearance, habits, tastes, and even susceptibility to various maladies. The fact that they are invariably of the same sex is a strong reason for believing that sex was already developed in the fertile ovum and consequently in the resulting blastomeres from that ovum.

The young of the nine-banded armadillo in a given litter are invariably of the same sex and are closely similar in all features (Fig. 32, p. 89). Newman and Patterson have shown that all the members of a litter come from the same egg. Patterson has established the fact that cleavage of the egg takes place in the usual manner, but later separate centers of development appear in the early embryonic mass and give rise to the separate young individuals.

Again in certain parasitic insects where one egg indirectly gives rise to a chain of embryos, or to a number of separate larvæ, possibly as many as a thousand, all of the latter are of the same sex. Even in some plants researches have shown that sex is already determined at the beginning of development. Then, too, much evidence has come to light recently showing that sex characters in certain cases behave as heritable characters and are independent of external conditions. Lastly there is visible and convincing evidence obtainable through microscopical observations that sex is determined by a mechanism in the germ-cells themselves.

The Sex-Chromosomes.—The evidence centers about a special chromosome or chromosome-group commonly designated as the *X-chromosome* or *X-element*, which has been found in various species of animals, including man. In the simplest case this chromosome is present in males in addition to the regular number of pairs, thus giving rise to an *uneven* instead of the conventional even number of chromosomes. This element remains undivided in one of the maturation divisions of the spermatocytes, in some forms in the first in others in the second, and passes

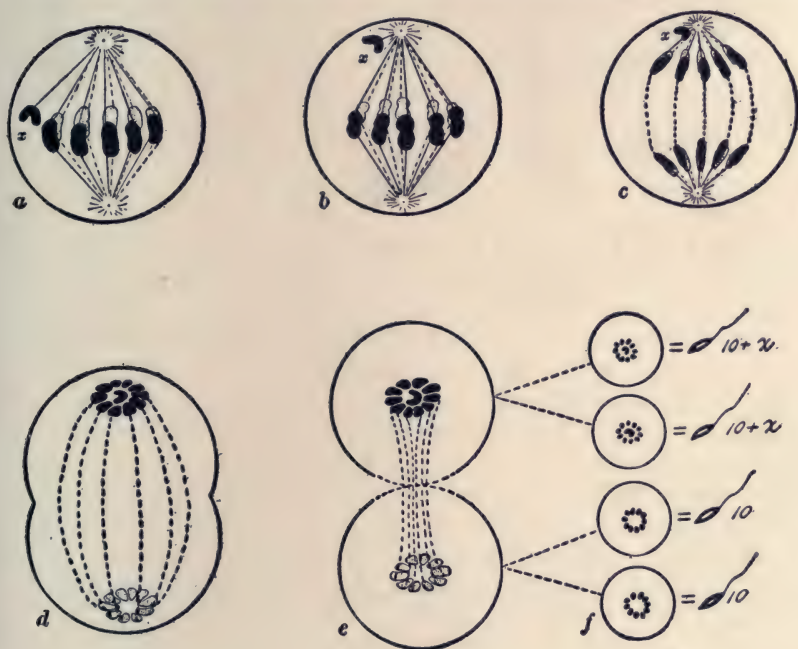


FIG. 39

Diagram illustrating the behavior of the *x*-element or sex-chromosome in the maturation of the sperm-cell. In one of the two maturation divisions (represented here as in the first) it passes undivided to one pole (*a*, *b*, *c*), in the other it divides. Since the cell without the *x*-element also divides the result is that ultimately from the original primary spermatocyte (*a*) four cells are formed (*f*), two with the *x*-element and two without it. Half of the spermatozoa therefore will bear an *x*-element, half will be without it. In *a* the ordinary chromosomes, arbitrarily indicated as 10, are supposed to have already paired for reduction so that the original diploid number in spermatogonia and body-cells of the male would be 20 plus the *x*-chromosome.

entire to one pole of the spindle (Fig. 39, p. 111). This results in the production of two classes of cells, one containing the *X*-element and one not. The outcome is that two corresponding classes of spermatozoa are produced. The phenomena involved are diagrammatically represented in Fig. 39. It has been clearly demonstrated that eggs fertilized by spermatozoa which possess this *X*-element, become females, those fertilized by spermatozoa which do not possess it always develop into males.

It has been found, furthermore, that in species in which the males possess this extra element the females have two of them. That is, if the original number in the somatic cells of the male were twenty-three, twenty-two ordinary (*autosomes*) and one *X*-element, the number in the somatic cells of the female would be twenty-four, or twenty-two autosomes and two *X*-elements. It has been found that when the chromosomes of the female pair for the reduction division, each chromosome uniting with its corresponding fellow, the two *X*-elements in the female pair in the usual way so that every egg-cell possesses an *X*-element. Thus every mature egg has an *X*-element, while only half of the spermatozoa have one. That is, if we assume twenty-three as the diploid number present originally in the somatic cells of the male and twenty-four as the number in the female, then one-half the spermatozoa of the male would contain the haploid number eleven, and the other half, the number twelve, whereas every mature ovum would contain twelve. Since there are equal numbers of the spermatozoa with the *X*-element and without it, and inasmuch as presumably under ordinary conditions one kind is as likely to fertilize the egg as the other, then there are equal chances at fertilization of producing a zygote with two *X*-elements or with but one.

Thus, Spermatozoon + *X* by Ovum + *X* = Zygote + *XX*.

Spermatozoon (no *X*) by Ovum + *X* = Zygote + *X*.

Or, to use the conventional designations of *n* for the haploid number of autosomes and of *2n* for the diploid number, $2n + X = \text{male}$, $2n + XX = \text{female}$.

It thus becomes possible to distinguish the sex of an embryo by counting the chromosomes of its cells. This has been accomplished in several cases.

In a number of species of animals the *X*-element in the male possesses a mate sometimes much smaller than itself, known as the *Y*-element. This is true in man (Fig. 40, p. 113) and certain

other animals, possibly in all mammals. The X - and the Y -chromosomes come into close contact during synapsis and in the ensuing division diverge to opposite poles, so that although the resulting spermatozoa have the same number of chromosomes, half of them have received the X -element and half the Y -element. The females, in such species, as in the simpler type, have two X -chromosomes. In other words in these forms the XY combination is male, the XX , female. That is, $2n + XY = \text{male}$, $2n + XX = \text{female}$.

This is well exemplified in the chromosomal behavior (Fig. 41, p. 114) of the fruit fly, *Drosophila melanogaster*, which has been so remarkably serviceable to both cytology and genetics. The somatic cells and unreduced germ-cells of this fly possess only

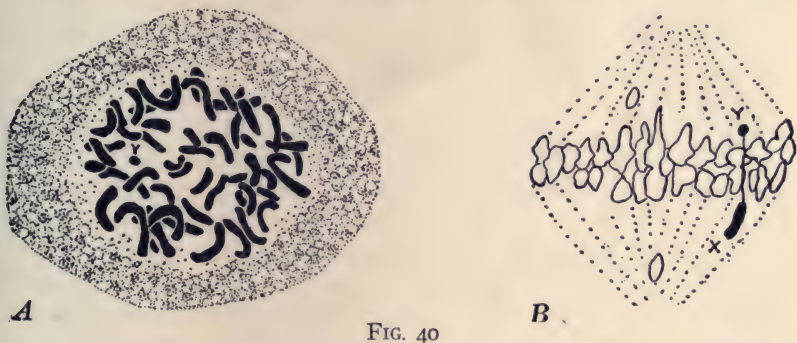


FIG. 40

A. Spermatogonial chromosomes (magnified about 2200 diameters) of a white man, showing chromosomes ready for division; the Y -chromosome of the sex chromosome pair is indicated by the letter Y . Which of the small rod-shaped chromosomes is the X -chromosome is not apparent.

B. Side view of first maturation division in a negro. The dividing autosomes are indicated in outline only; the sex chromosomes, marked X and Y , are shown in black.

eight chromosomes, three pairs of autosomes and a pair of sex chromosomes—the latter shown in black in Fig. 41. One pair of the autosomes is very small. The cells of the female possess two rod-like X -chromosomes. In the male the simple X -chromosome is accompanied by a hook-shaped Y -chromosome. The diagram (Fig. 41) shows the result of the reduction division and of the subsequent fertilization. Every egg, after reduction, has an X -chromosome but there are two classes of spermatozoa, one having an X -chromosome and the other a Y -chromosome. Since each kind has an equal chance to fertilize eggs, half of the

eggs are fertilized by X -sperm and half by Y -sperm. As already explained, the XX -zygote is a female, the XY -zygote, a male.

Professor Wilson thinks it probable that the first type, in which males have only a single sex-chromosome, has arisen by the gradual disappearance of the Y -element. In different though related species of insects, he found various gradations between those in which the Y -element is almost or quite as large as the

X -element to those in which it is very minute. In one species, indeed, while usually present, in some individuals he found it might be absent without visibly affecting sex or sexual characteristics.

This may account for the discrepancies in the spermatogonial chromosome counts in man, where in some of the more recent investigations forty-seven, in others forty-eight have been reported. Inasmuch as the chromosome lacking in the lesser count is the Y -element, it seems probable in such cases that the small Y -element has simply been overlooked or has been obscured by the other chromosomes. However this may be, Painter, who has done the most extensive work in this field, has preparations of both negroes and whites

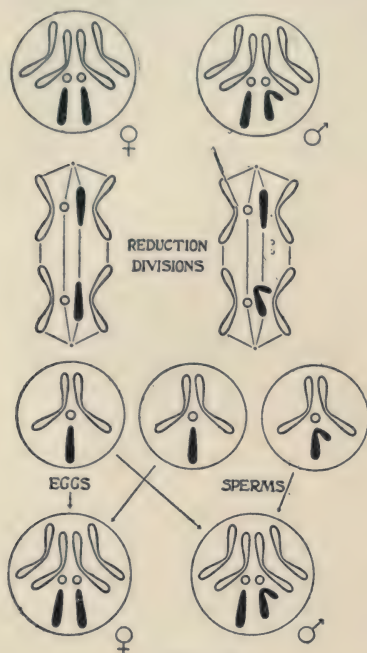


FIG. 41

Diagram to show chromosome relations in the inheritance of sex in *Drosophila melanogaster* (after Babcock and Clausen).

both can be seen (Fig. 40, p. 113).

A differential pair of chromosomes supposed to be sex chromosomes has recently been discovered in several dioecious flowering plants. Allen demonstrated in 1919 that the female gametophyte of the liverwort, *Spharocarpus*, is characterized by the presence of a large X -like chromosome, and the male gametophyte, by a corresponding small Y -like chromosome.

Reversal of Conditions in Moths and in Fowls.—A curious reversal of conditions, evidenced by the behavior of certain hereditary characters associated with the sex-chromosomes, and in part by the appearance of the chromosomes themselves, occurs in certain moths, in fowls and possibly in some fishes. Here the pair of special chromosomes characterizes the male, the single sex-chromosome the female, or in other words every mature spermatozoon possesses the special element but only half of the ova have it. When two kinds of spermatozoa are present the male is said to be *digametic*, but in these forms where conditions are reversed it is the female which is digametic.

Since it is uncertain whether physiologically the sex-chromosomes in such cases are strictly comparable to the sex-chromosomes in male digamety, instead of calling them X- and Y-chromosomes most cytologists are inclined to be non-committal and give them other symbols as Z and W. The formulæ in these cases are thus commonly written $2n + ZZ = \text{male}$, and $2n + Z$ (or $+ ZW$) = female. The cytological demonstration of the Z-chromosomes has been most clearly worked out in certain moths. The chromosomes of fowls are peculiarly difficult to study yet in both the germinal and somatic tissues of male embryos there are two characteristically large curved elements (Fig. 42A, p. 116), and in the corresponding tissues of female embryos one similarly large, curved element, (Fig. 42B) which fit the requirements of the genetical evidence to be mentioned later.

In moths, Seiler has demonstrated that half of the ova extrude the Z-chromosome undivided with the first polar body and half of them retain it. Presumably the two types of ova are produced in the same way in fowls although this has never been observed. By modifying the temperature during the maturation period of the moth's ova Seiler found he could alter the sex ratio, probably by influencing the retention or expulsion of the Z-chromosome. Possibly other deviations in sex ratio from the normal 50:50 proportion are explicable upon a similar basis.

Complexity in Certain Forms.—In some instances the conditions may be more complex than the ones indicated but the principle remains the same throughout; the very complexity when understood strengthens rather than weakens the evidence. The X-chromosome may be temporarily or permanently linked to another chromosome (autosome), or, with or without a Y-mate,

it may be a compound in which it is represented by a group of separate chromatic bodies that act as a unit during gametogenesis.

A formidable difficulty seemed at one time to present itself in the case of such forms as the phylloxerans and aphids which some times reproduce parthenogenetically, at other times sexually. Females only are produced from fertilized eggs. The interesting discovery was made, however, by Morgan in *Phylloxera* and by Baehr in *Aphis* that while half of the spermatocytes receive the X-element and half do not, the latter or male-producing type never come to maturity. On the other hand, in these forms both males and females develop from parthenogenetic eggs. It was found both by Morgan and Baehr that the males have the



FIG. 42

A. Section of early germ-cell in male chick embryo showing two characteristic chromosomes, marked Z, which are probably to be interpreted as the sex chromosomes.

B. Corresponding cell from female chick embryo where the chromosome marked Z is presumably the single sex chromosome.

characteristic lesser number of chromosomes, the females the increased number, and Morgan's observations make the conclusion practically certain that the difference in chromosome number is brought about at the time of the extrusion of the single polar body. Here it is clear that something within the egg itself—the something which determines the retention or expulsion of the X-element—is the determining factor of sex. Even before the extrusion of the polar body, indeed, the male-producing egg is distinguishable by its smaller size.

Sex Chromosomes and Sex Determination.—What the sex chromosomes signify in connection with sex determination has

never been clearly shown. It seems probable that sex is the resultant of several essential factors and is not established normally unless all work together, the *X*-chromosome, when the male is the digametic sex, being a fundamentally important factor. That the *Y*-chromosome is not universally necessary in sex-production is manifest, since it is lacking in many species of animals.

The tendency at present is toward regarding sex as due to a certain balance of factors with the sex-chromosomes, under usual conditions, serving as the regulative elements. With an upset of normal conditions, however, such as is known to occur occasionally through irregularities in the distribution of the chromosomes at the time of reduction, sex abnormalities result. Thus Bridges has found that in certain triploid races of *Drosophila* in which the normal relation of autosomes and *X*-elements is disturbed, a preponderance of either results in characteristic sex abnormalities. Individuals which were triploid in all respects including three *X*-chromosomes scarcely differed from normal diploid females, but if they were triploid with respect to autosomes and had only two *X*-chromosomes the individuals were larger, differed otherwise from normal forms, and were *sex intergrades*. On the other hand females with three *X*-chromosomes but otherwise diploid, were sterile and of low viability, and exhibited abnormal somatic characters. Triploid individuals with but one *X* were males showing characteristic peculiarities. Such facts make it plain that sex does not depend alone on the sex-chromosomes, but that the autosomes are also involved. The outcome is the joint effect of all the chromosomes and the balance is swung toward the male side or the female side apparently as the result of the quantitative relations between the *X*-chromosomes and the autosomes. The physiological relations involved are unknown although at bottom there appear to be fundamental differences of metabolism between the sexes. The familiar fact that one sex frequently possesses in rudimentary form organs that are fully developed and functional in the opposite sex, such as the nipples of male mammals, and the occurrence of such conditions as intersexuality and hermaphroditism, lead toward a belief in the existence of specific male-determining and female-determining substances in the same individual, with the balance of power ordinarily wielded by the sex-chromosomes. In some way in the general metabolic processes of the body, the chromatin

of the sex-chromosomes acts apparently as an initiatory, modifying or controlling factor with regard to sexual differences.

SEX-LINKED CHARACTERS

The discovery of the remarkable behavior of certain characters in heredity which can only be plausibly explained by supposing that they are linked with a sex-determining factor still further strengthens our belief in the existence of such a definite factor. Such characters are commonly termed *sex-linked* characters. These should not be confused with *sex-limited* traits, such as the beard or other secondary sexual characteristics of mankind, which, probably through the influences of hormones from the reproductive glands, are fully expressed in one sex only.

Sex-Linked Characters in Man.—Since there are a number of sex-linked characters in man we may choose one of these, such as color-blindness, for illustration. The common form of color-blindness known as Daltonism in which the subject can not distinguish reds from greens, a condition which seems to be due to the absence of something which is present in individuals of normal color vision, is far commoner in men than in women. Its type of inheritance, sometimes termed “crisscross” heredity, has been likened to the knight moves in a game of chess. The condition is transmitted from a color-blind man through his daughter to half of her sons. Or, to go more into detail, a color-blind father and normal mother have only normal children whether sons or daughters. The sons continue to have normal children but the daughters, although of normal vision themselves, transmit color-blindness to one-half of their own sons. If such a woman marries a color-blind man, as might easily happen in a marriage between cousins, then as a rule one-half her daughters as well as one-half her sons will be color-blind.

In such cases what appears to be a mysterious procedure becomes very simple if we assume that the defective character is associated with the sex-determining factor, or to make it concrete let us say with the X-element. The chart shown in Fig. 43, p. 119, indicates what the germinal condition would be under the circumstances. The column to the right represents the paternal, the one to the left the maternal line. Since XX means female and XY male, and inasmuch as we have assumed that the physical basis of the defect to which color-blindness is due is conveyed by the X-element, we may represent the defective

single X of the male in outline only (see first row.) It is obvious that after the reduction divisions (second row) the mature sex-cells of the female will each contain a single normal X , the corresponding sex-cells of the male will contain either Y or a defective X . Since if any member of the class of spermatozoa containing Y fertilizes an egg the resulting zygote (row three) will have but one X and that a normal one, the individual

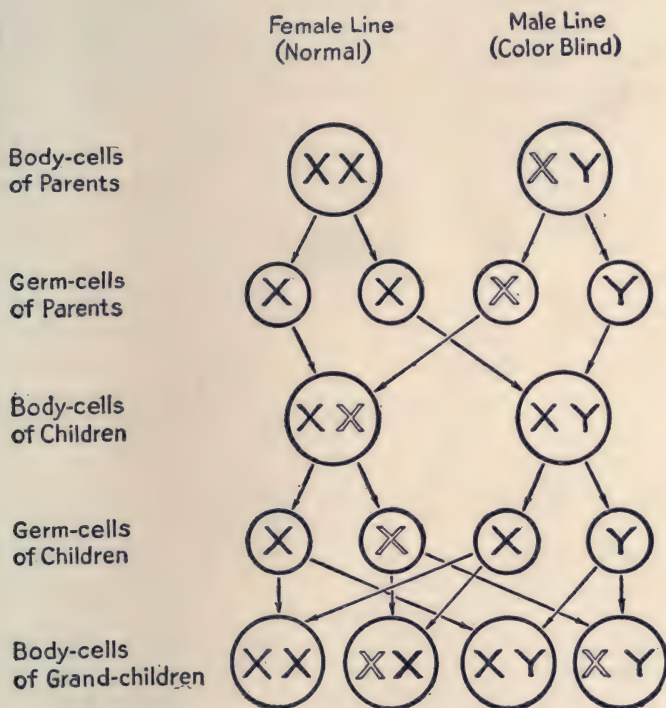


FIG. 43

Diagram illustrating the inheritance of a sex-linked character such as color-blindness in man on the assumption that the factor in question is located in the X -chromosome. The normal X -chromosome is indicated by a black X , the one lacking the factor for color-perception, by a light X . It is assumed that a normal female is mated with a color-blind male.

which develops from the zygote will be normal as regards color vision and moreover will be male because the condition one X always means maleness. On the other hand, if any member of the class of spermatozoa containing the defective X fertilizes

an egg two X -elements are brought together and this of itself means femaleness. In this case one of the X -elements is defective but the single normal X is sufficient in itself to produce normal color vision. But when it comes to the maturation of the sex-cells of this female, the pair of X -elements are separated in the usual way with the result that half of the mature ova contain a normal X and half a defective X (row four). Since in a normal male, however, the mature reproductive cells will contain either a normal X or Y (fourth row), any one of four different kinds of matings may result. A sex-cell carrying normal X of the male may combine with an ovum containing normal X producing a normal female (row five). Or such a cell may combine with an ovum carrying the defective X , also producing a female but one who although of normal color vision herself, like her mother, is a carrier of the defect. On the other hand, any one of the spermatozoa without an X may combine with an ovum containing the normal X , in which case a normal male is produced and, moreover, one who, like his mother's brothers, is incapable of transmitting the defect. However, the Y -bearing sperm-cell is just as likely to fertilize an ovum carrying the defective X , in which event the resulting individual, a male, must be color-blind because he contains a single X , and that defective. In other words, the chances are that one-half the sons of a woman whose father was color-blind will be color-blind, the other half perfectly normal; and that all of the daughters will be of normal color vision although one-half of them will probably transmit the defect to one-half of their sons. From a glance at the diagram it is readily seen also that a color-blind female could result from the union of a color-blind man (see first row) and the daughter of a color-blind man (see third row). For half of the gametes of such a female would bear the defect as would also that half of the gametes of the male which carry X , hence the expectation would be that half of the daughters of such a union would be color-blind and half would be carriers of color-blindness; and that half of the sons would be color-blind and half normal. All the sons of a color-blind woman would be color-blind because she has only defective X -elements to pass on.

Various other conditions in man have been reported as following more or less accurately the same course in inheritance as color-blindness. Among these may be mentioned: *hemophilia*, a serious condition in which the blood will not clot properly, thus

rendering the affected individual constantly liable to severe or fatal hemorrhage; near-sightedness (*myopia*) in some cases; a degenerative disease of the spinal cord known as *multiple sclerosis*; congenital fissure of the iris or other parts of the eye (*coloboma*); abnormal smallness of eyes (*microphthalmia*); a continuous rolling movement of the eyeball (*nystagmus*); pattern baldness; hereditary toothlessness; deficiency in sense of smell; progressive atrophy of the optic nerve (*neuritis optica*); Gower's *muscular atrophy*; some forms of *night-blindness*; in some cases *ichthyosis*, a peculiar scaly condition of the skin; and apparently certain temperamental states such as "Wanderlust" and sea-lust.

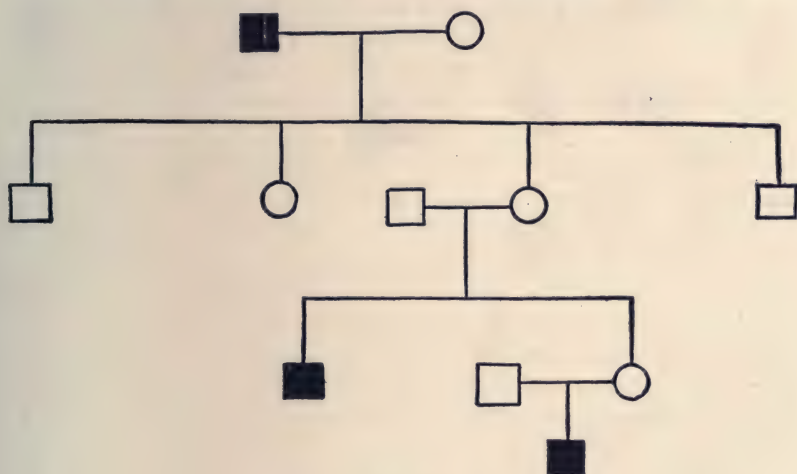


FIG. 44

Chart showing the inheritance of a case of syndactyly after the manner of a sex-linked character. The affected individuals are represented in black; squares indicate males, circles females. The condition is seen to be inherited by males through unaffected females.

In one of my own tabulations of a case of inheritance of "webbed" digits or *syndactyly*, a condition in which two or more fingers or toes are more or less united, a sex-linked inheritance is clearly indicated (Fig. 44), although from the pedigrees recorded by other investigators this condition usually appears in some of both the sons and daughters of an affected individual. In one family, however (Schofield family), webbed toes has been reported as if transmitted by the Y-chromosome; that is, from father to son, independently of the female line. Where a particular character

thus varies in its mode of transmission it probably has a different cause in the germ, the gene of which lies in a different chromosome.

The Occurrence of Sex-Linkage in Lower Forms Renders Experiments Possible.—The course followed by such characters in man can be inferred only from the pedigrees we can obtain from family histories. Fortunately, however, such sex-linkage also occurs in lower animals and we are able therefore to verify and extend our observations by direct experiments in breeding. Over forty sex-linked characters have been found to exist in the fruit fly known as *Drosophila melanogaster*. Extensive breeding experiments with this fly by Professor T. H. Morgan and his associates have borne out remarkably the interpretation that the characters in question are really linked with a sex-determining factor; that is, their genes lie in the X-chromosome.

The normal eye-color in *Drosophila*, for example, is red, but Professor Morgan found white-eyed males appearing in his strain. This white-eyed condition proved to be sex-linked. It is confined to the males unless a red-eyed female, the daughter of a white-eyed male and therefore a carrier of the unusual condition, is bred to a white-eyed male. In the latter event one-half of the females of the next generation are white-eyed. Inasmuch as a single pair of these flies produces from two to three hundred offspring at a time and a new generation can be secured every ten or eleven days, such material affords a remarkable opportunity, by making reciprocal crosses of normal red-eyed females by white-eyed males and white-eyed females by red-eyed males, to test out the hypothesis of linkage of the character with the sex-determining factor. The former cross should, if the hypothesis is correct, produce only red-eyed offspring, and the latter, red-eyed females and white-eyed males. White-eyed females mated to white-eyed males should produce only white-eyed progeny. The experimental results confirm this prediction. If the defect represented in Fig. 43, p. 119, be supposed to be such a white-eyed condition instead of color-blindness the diagram will serve equally well to indicate its manner of inheritance.

Other conditions which have appeared such as unusually short wings, yellow wing- and body-color and the like (see chromosome I, Fig. 74, p. 195) follow the same course when tested. Several sex-linked *lethal* factors—factors which are associated

with early death—have appeared in *Drosophila*. These reside apparently in the sex-chromosome. All males which receive an *X*-chromosome bearing such a lethal, die; females which have it in both *X*-chromosomes die, but those which have one normal *X*-chromosome survive.

Evidence that the *Y*-chromosome carries genes is very scanty. Some three or four cases of a peculiar type of inheritance from male parent to male offspring (some but not all cases of webbed toes in man, and pigment spots in certain fish) indicate transmission in this element but, beyond the fact of its occurrence in various species of animals, little is known about the *Y*-chromosome. Bridges has shown in cases of abnormal chromosome distribution that zygotes of the *YY* (no *X*) type are not viable and that males of the *XO* (i. e., no *Y*) type are sterile.

Reversed Conditions in Certain Forms.—In the case of fowls, canaries, ducks and pigeons, as well as some moths, sex-linked characters have been discovered which are transmitted in just the reverse order to that seen in man or in *Drosophila*; that is, they are inherited as if the female carried a single sex-determining element and the male two. The chromosomal basis for this has already been indicated (p. 115). Barring, for example, such as is seen in the Plymouth Rock breed of poultry, is a dominant sex-linked trait which behaves as if the female were the digametic (i. e., *ZW* or *ZO*) type and the male the homogametic (*ZZ*) type. When the barring factor is present even as a single gene it is expressed, or in other words, it is *dominant*. Thus when a barred male is crossed with a black female all the offspring are barred and when these are interbred all the male progeny are barred, while half of the female progeny are barred and half are black. This is just the reverse genetical condition to that shown in Fig. 43. In the reciprocal cross of black male by barred female, the male offspring, since one of the sex chromosomes which they bear carries the factor for barring, are barred. Interbreeding of this generation produces one in which half of the males and half of the females are barred, and half are black. The females from black male by barred female, however, have each but a single *Z*-chromosome and since it came from their black father they are black.

The Secondary Sexual Characters.—The fundamental difference between the sexes is that the female is an egg-producer, the male, a sperm-producer. In many animals, however, the

sexes differ also in external appearances. These differences may be confined to structures which are associated directly with reproduction or may include such characters as color, song, ornamentation and the like. All sex differences not restricted to gamete-production are called *secondary sexual characters*. In the discussion of hormones the necessity of secretions from the gonad for the normal development of the secondary sexual characters has already been pointed out. Presumably both male and female have genes for the secondary sexual characters of each sex in their autosomes, but for these to develop appropriately into the respective male or female type requires both the stimulus and guidance of the proper sex-chromosome combination in the body-cells and the endocrine secretion of the gonad. Through castration or gonad-transplantation the suppressed secondary sex genes of the opposite sex may be released or stimulated into activity.

Alterations of Sex.—While in general biologists, on the evidence of the sex-chromosomes, regard sex as *determined*, in the usual sense of the word, at the time of fertilization, it is evident that *sex differentiation* is subject to modification or even reversal if the normal sex tendency is disturbed by internal conditions such as chromosome irregularities or by such other factors as absence or changes in the hormones of the sex glands.

A few instances of complete sex reversal in birds have been reported. Thus Crew describes a hen, the mother of chickens, which ceased to lay, gradually assumed the characteristics of the male—crowing, comb, wattles, spurs, plumage (after moulting) and behavior—and the following spring mated with hens and, in a test case, became the father of two chicks. A post-mortem examination showed that not only had the ovary (single in fowls) been almost wholly destroyed by tuberculosis and replaced by a tumor, but that two functional testes were present. Riddle records the transformation of a female ring-dove into a male. Here, similarly, a tubercular infection had destroyed the ovary and two well-formed testes had developed.

Riddle, indeed, has for years been conducting experiments on the size, chemistry and stored energy of the egg which indicate that sex can be controlled in pigeons by regulating egg production. He reports that the female-producing egg is larger, has a greater amount of stored food, a lower water content, and a lower rate of metabolic activity than the male-producing egg. Two eggs are laid at each nesting time and in wild species one

of these commonly develops into a female, the other into a male. If the eggs are removed, however, before the female begins to incubate them, she will lay a larger number of eggs than she would otherwise do. Most of these are female-producing and toward the end of the season all may be so. With poultry Jull has obtained a somewhat similar result. He found that the early eggs laid by pullets produced an excess of males (approximately 63 per cent.) but that the proportion of male offspring diminished steadily—to about 32 per cent. after 100 eggs had been laid—with the increasing period of egg production. Jull points out that the facts are reconcilable with the chromosomal theory of sex determination if one postulates that in the early eggs of pullets the *W*-chromosome which supposedly characterizes the female-producing eggs is extruded into the polar-body more frequently than the *Z*-chromosome, and that later the reverse condition occurs.

In frogs Richard Hertwig observed that stale eggs—eggs not fertilized until from 68 to 77 hours after laying—produced a large excess of males (673 males to 13 females in one experiment, with a heavy mortality), whereas eggs of the same female when fertilized immediately produced approximately equal numbers of males and females. Hertwig, assuming *XX* to represent the female condition, thought it probable that over-ripeness weakened the action of one of the *X*-chromosomes. Miss King found that in toads by slightly drying the eggs or by extracting water from them with any one of various chemical solutions the proportion of females was increased. Because of the uncertainty in recognizing the sex of tadpoles or of young toads or frogs, however, the evidence from such forms is by some biologists regarded as inconclusive. Again, in cultures of rotifers which are reproducing only parthenogenetically and which consist therefore of parthenogenetic females alone, Shull and Whitney have each shown that males could be made to appear by a suitable change in diet. Here, however, sex was not reversed but parthenogenetic females were stimulated to produce both males and sexual females in addition to females of their own type. Whitney has shown farther that in several species of rotifers an abundant diet results in as high as 95 per cent. of male offspring in the second filial generation, while with a scant diet only female offspring are produced. In the sex determination of such parthenogenetically-produced individuals Shull regards the effect as due to

influences operative during the maturation of the egg from which the sexual individual's mother develops.

Such facts as the foregoing together with the conditions known to exist in the free-martin (p. 84) indicate that although probably the chromosomal mechanism ordinarily gives the developing individual an impetus toward maleness or femaleness, sex is not irrevocably fixed by it but may be altered more or less by other factors.

Statistics show that in man, in the white race at least, more males are born than females. The sex ratio varies in different countries from 101 to 107 males to each 100 females. To explain this on the basis of the chromosome theory it might be supposed that the male-producing class of spermatozoa are more active or have greater vitality than the female-producing class. It is evident that alternation of the sex ratio might also be brought about if some outside influence which favored one class of spermatozoa more than the other were brought to bear upon them. In the fruit fly *Drosophila* certain lethal factors have been discovered which cause the early death of those individuals in which the lethal gene is not offset by a normal one. Clearly such a condition in the sex-chromosome would modify sex ratios. In man mortality is greater in male infants both before and after birth than in female infants.

CHAPTER VIII

MENDELISM

New Discoveries in the Field of Heredity.—Writing in 1899, one of America's well-known zoologists asserts that, "It is easier to weigh an invisible planet than to measure the force of heredity in a single grain of corn." And yet only two or three years later we find another prominent naturalist saying regarding heredity that, "The experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry." Again, "The breeding pen is to us what the test-tube is to the chemist—an instrument whereby we examine the nature of our organisms and determine empirically their genetic properties." Here is a decided contrast of statement and yet both were justifiable at the time of utterance. For even at the writing of the first statement the investigations were in progress which, together with the rediscovery of certain older work, were to transfer our knowledge of heredity from the realm of speculation to that of experiment and disclose certain definite principles of genetic transmission.

Through a knowledge of these principles in fact, the shifting of certain characters is reducible to a series of predictable proportions and the skilled breeder may proceed to the building up of new and permanent combinations of desirable characters according to mathematical ratios and, what is of equal importance, he can secure elimination of undesirable qualities. While there are many limitations in the application of these principles and while new facts and modifications are constantly being discovered concerning them, nevertheless they represent the first approximations to definite laws of hereditary transmission that we have ever been able to make. The practical fact confronts us that whatever our theoretical interpretations may be, the principles are so definite that through their application important improvements of crops and domesticated animals have already actually been secured and one may confidently expect still others to follow.

Mendel.—The principles involved are called the Mendelian principles after their discoverer, Gregor Johann Mendel, abbot of a monastery at Brünn, Austria. After eight years of patient experimenting in his cloister garden with plants, chiefly edible peas, he published his results and conclusions in 1866, in the *Proceedings of the Natural History Society of Brünn*. While known to a few botanists of that day, the full importance of the contribution was not recognized, and in the excitement of the post-Darwinian controversy, the facts were lost sight of and ultimately forgotten.

Rediscovery of Mendelian Principles.—In 1900 three men, Correns, De Vries and Tschermak, working independently—in different countries, in fact—rediscovered the principles and called attention anew to the long-forgotten work of Mendel which they had come upon in looking over the older literature on plant breeding. These investigators added other examples from their own experiments. Since their rediscovery the principles have been confirmed in essential features and extended by numerous experimentalists with regard to a wide range of hereditary characters in both animals and plants.

While the science of genetics during the past twenty-five years has advanced so far beyond the simple though all important foundation laid by Mendel that this brilliant founder would himself scarcely recognize certain aspects of it in its present form, nevertheless the restrictions or the elaborations that more recent knowledge makes necessary in no wise nullify his original discoveries.

Independence of Inheritable Characters.—It has been found that many truly heritable characteristics or traits of an individual, whether plant or animal, are comparatively independent of one another and may be inherited independently. Where there are contrasted characters in father and mother, such as white plumage and black plumage in fowls, smooth coat and wrinkled coat in seed, horns and hornlessness in cattle, long fur and short fur in rabbits, beard and beardlessness in wheat, albino condition and normal condition, etc., there is obviously a bringing together of the genes of the two traits in the resulting offspring. In the third generation, however, in the progeny of these offspring, the two distinct characters may be set apart again, thus showing that in the second generation while perhaps one only was visible, the factors which determine both were nevertheless present, and moreover, they were present in a separable condition.

The fundamentally important discovery of Mendel was this unitary nature of the inheritable characteristics with which he worked, and their independence in heredity. He showed conclusively that they could be itemized as distinct units which could be brought together in one generation and segregated in a later one. An important qualification that the modern geneticist has to make, as we shall see later, is that this independent assortment of characters is not complete since certain characters introduced together into a cross tend to remain together in subsequent gen-

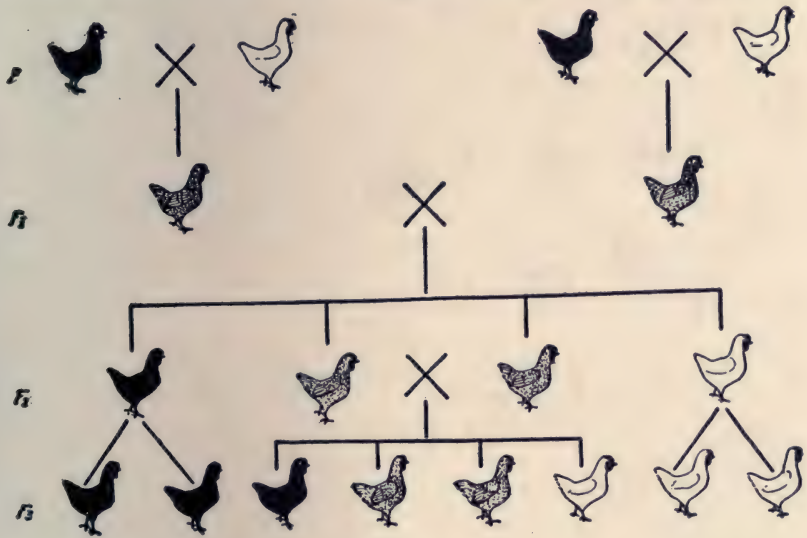


FIG. 45

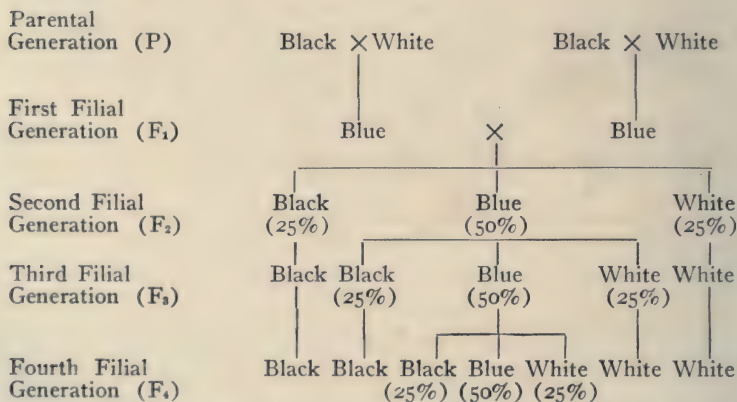
Diagram showing the scheme of inheritance in the blue Andalusian fowl.

erations. They are members of a group which in heredity behaves independently of other groups. Such characters exhibit what is known as "linkage."

Illustration of Mendelism in the Andalusian Fowl.—Let us take as a simple example the case of the Andalusian fowl. Although it is not one established by Mendel it illustrates certain of the essential conditions underlying Mendelism in a more obvious way than the cases worked out by Mendel himself. The so-called blue Andalusian fowl results from a cross of a color variety of the fowl which is black with one which is white with

black-splashed feathers. The result is the same irrespective of which parent is black. When bred with their like, whether from the same parents or different parents, these blue fowls produce three kinds of progeny, approximately one-fourth of which are black like the one grandparent, one-fourth white like the other grandparent, and the remaining half, blue like the parents (Fig. 45, p. 129). Moreover, the black fowls obtained in this way will, when interbred, produce only black offspring and the same is true of the white fowls. To all appearances as far as color is concerned they are of as pure type as the original grandparents. With the blue fowls, however, the case is different, for when bred together they will produce the same three kinds of progeny that their parents produced and in the same proportions. Again the white and the black are true to type but the blue will always yield the three classes of offspring and this through generation after generation.

The facts may be illustrated graphically as follows where the word "black" indicates the original black parent, "white" the original white (black splashed) parent and "blue" the hybrid offspring.



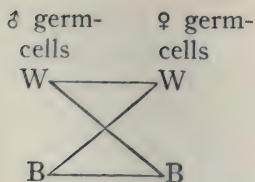
The Cause of the Mendelian Ratio.—Concerning the cause of this peculiar ratio of inheritance in crossed forms Mendel suggested a simple explanation. Animals or plants that can be cross-bred, obviously must be forms that produce a new individual from the union of two germ-cells, one of which is provided by each parent. Mendel, who worked exclusively with plants, expressed the idea that there must be some process of

segregation going on in the developing germ-cells of each hybrid whereby the factors for the two qualities are set apart in different cells with the result that half of the germ-cells of a given individual will contain the determiner of one character and half, the determiner of the other. That is, a given germ-cell carries a factor for one or the other of the two alternate characters but not the factors for both. In a plant, for example, in the male line, half of the pollen grains would bear germ-cells carrying the determiner of one character and half, that of the other. Similarly in the female line, half of the ovules would contain the determiner of the one character and half, that of the other. Likewise in animals as regards such pairs of characters there would be two classes of germ-cells in the male and two in the female. In the case of the blue Andalusian fowls under discussion this would mean that half of the mature germ-cells of the male carry the black-producing factor, and half carry the white-producing factor, and the same is true of the germ-cells of the female. Thus when two such crossed forms are mated, there are, by the laws of chance, four possible combinations, namely: (1) white-determining sperm-cell and white-determining ovum; (2) white-determining sperm-cell and black-determining ovum; (3) black-determining sperm-cell and white-determining ovum; and (4) black-determining sperm-cell and black determining ovum. Manifestly, the first combination can only give white offspring; the second, white and black, gives blue (by such a cross the original blues were established); likewise, the third, black and white, gives blue; and the fourth combination can only give black offspring. This matter may be graphically represented by the following formulæ in which B indicates the determiner of Black in the germ-cell and W the determiner of White: ♂ signifies male; ♀ female.

IN THE ORIGINAL PARENTS

$$W \times B = WB = \text{Blue}$$

IN THE HYBRIDS



or

♂	♀	
W	W	= WW = White
W	B	= WB = Blue
B	W	= BW = Blue
B	B	= BB = Black

Thus of the four possible combinations one only can produce white fowls, two (WB or BW) can produce blue fowls, and one black fowls. That is, the ratio is 1:2:1 or the 25, 50 and 25 per cent., respectively, of our diagram. The black fowls or the white fowls will breed true in subsequent generations when mated with those of their own color because the determiner of the alternative character has been permanently eliminated from their germ-plasm; but the blue fowls will always yield three types of offspring because they still possess the two classes of germ-cells.

Verification of the Hypothesis.—The hypothesis that germ-cells of crossed forms are of two classes with respect to a given pair of Mendelian characters is further substantiated by the following facts. If in the case of the fowls under discussion one of the blue fowls is mated with an individual of the white variety, half of the progeny will be blue and half, white. For the hybrid has two kinds of germ-cell, black-producing, which we have designated by the letter B, and white-producing (or W) in equal number while the white parent has only one kind, white-producing. It is obvious that if half the germ-cells of the hybrid form are of the type B then half the progeny will be of the BW type, which is blue, and the other half will be of the WW type, which is white. In the same way if we mate a hybrid and a black fowl, half of the progeny will be black and half will be blue, that is, there could only be WB and BB types.

The fact must not be lost sight of that since the pairings are wholly determined by the laws of chance the proportions are likely to be only approximate. It is obvious that the greater the number of individuals, the nearer the results will approach the expected ratio.

DOMINANT AND RECESSIVE

One Character May Mask the Other.—In a large number of cases, however, the actual condition of affairs is not so evident as in the Andalusian fowl, for instead of being intermediate or different in appearance, the generation produced by crossing resembles one parent to the exclusion of the other. Such an overshadowing is spoken of as *dominance*, and the two characters are termed *dominant* and *recessive*. Thus when brown ring-doves and white ring-doves are mated the progeny are all brown, or if wild gray mice are mated to white mice the progeny are all gray. So black is dominant to white in rose-comb bantams;

brown eyes to blue eyes in man; beardlessness to beard in wheat, and likewise rough chaff to smooth, and thick stem to thin; tallness to dwarfness in various plants; normal condition to the peculiar waltzing condition in the Japanese waltzing mouse. Numerous other cases might be cited but these are sufficient to illustrate the condition.

Segregation in the Next Generation.—But now the question arises, what do such crosses as show dominance transmit to the next generation? Experiments show regarding any given pair of these alternate characters that they are set apart again

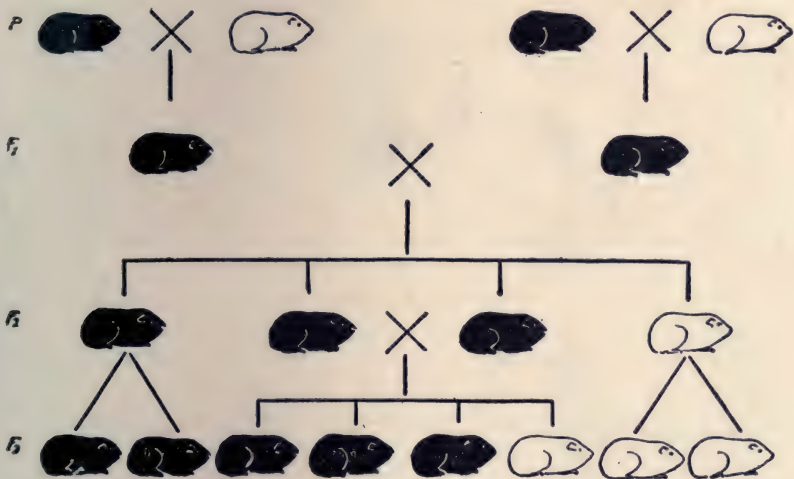


FIG. 46

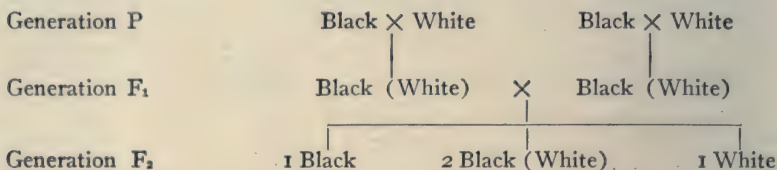
Diagram showing the scheme of inheritance in guinea-pigs when black and albino forms are crossed.

in the succeeding generation, returning in a definite percentage to the respective grandparental types.

Dominance Illustrated in Guinea-Pigs and in Cattle.—In guinea-pigs for example (Fig. 46, above), when an individual (either male or female) of a black variety, is crossed with one of an albino white strain, the F₁ generation are all black like the black parent. When these are interbred or bred with other blacks which have had one black and one white parent, only two visible types of progeny appear, viz., black and white, and these approximately in the ratio of three to one.

Analysis by further breeding shows, however, that there are in reality three types, but since dominance is complete the pure extracted dominant and the mixed dominant-and-recessive type are indistinguishable to our eye. That is, while the blacks are three times as numerous as the whites, two out of every three of these blacks are really hybrid and correspond to the blue fowls of our former example.

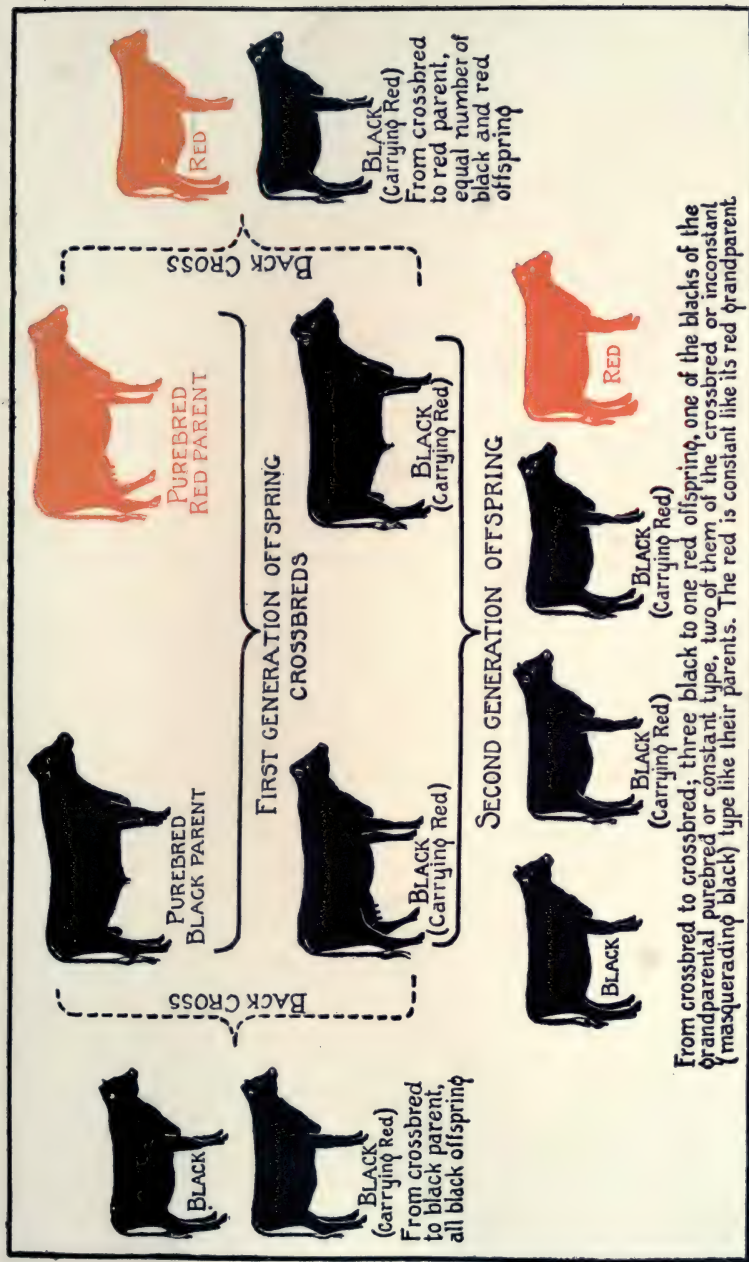
The condition is readily comprehended when expressed diagrammatically thus:



In other words the germ-cells of the one original parent (Generation P) would contain only determiners for black and that of the other parent would contain only determiners for white. The condition of the individuals produced by the cross would be represented by the formula B(W). But these determiners segregate in the germ-cells of the crossed form, whether it be male or female, into B and W. Hence half the spermatozoa of the male hybrid (generation F₁) would carry the B determiners and half the W determiners. The same is true of the mature ova of the female hybrid. Consequently, in mating there are always four equally possible combinations, viz., BB, B(W), (W)B, and WW. Since B is dominant three out of the four matings would yield black individuals, or in other words the ratio would be 3:1.

The pure blacks when mated together will breed true in subsequent generations, likewise the whites, but the blacks carrying white as a recessive will yield when interbred the same ratio of whites and black as did their hybrid parents (Fig. 46, p. 133).

The same principle is illustrated in cattle in Fig. 47, on the facing page. Except where complicating factors, such for example as produce brindle, are present, a cross between a red animal (*e. g.* Red Polled) and a black one, such as an Angus, gives black offspring. A mating of two such crossbred blacks one to another yields three blacks to one red. Only one of the three, however, will breed true to black. A back-cross of black which carries red,



From crossbred to crossbred; three black to one red offspring, one of the blacks of the grandparental purebred or constant type, two of them of the crossbred or inconstant (masquerading black) type like their parents. The red is constant like its red grandparent

FIG. 47. Diagram of inheritance of black and red in cattle (after Cole and Jones; *Bulletin 113*, Agricultural Experiment Station, University of Wisconsin).

to a pure-bred black individual gives all black offspring, and a back-cross of such a carrier of red to a pure-bred red individual gives equal numbers of red and of black offspring (Fig. 47). It is clear from such examples that appearance can not be used as a reliable guide in breeding since an individual may pass on traits not revealed in its own body.

This very fact of dominance of one color over another has, indeed, often been a matter of much concern in practical breeding as when a red or a red-and-white calf has appeared in black or in black-and-white breeds of cattle. American Holstein breeders, for instance, are so strongly prejudiced against red-and-white animals of this breed that such calves can not be entered in the American herd-book. If a bull is known to have sired red-and-white calves his commercial value as a breeding animal is almost wholly destroyed, notwithstanding the fact that such offspring may be up to the best in all other standards that distinguish this breed. As a matter of fact where such red or red-and-white calves are thrown each parent is equally responsible since red is a recessive and can only reappear when each black parent is a carrier of red (Fig. 47). In a study of such occurrence of red calves in black breeds, Cole and Jones point out that cattle of the Holstein-Friesian breed were largely red-and-white up to 1750, and that the black-and-white cows became popular in Holland only after such types had been introduced from Jutland. The authors also state that the Aberdeen-Angus breed is believed to have been of black foundation with red crosses and that the Galloway breed has a somewhat similar origin. Since certain individuals in such black breeds may still be carrying red it is evident that, from a mating of two such carriers, the expectation is that one out of four of the offspring will be red. Other unit characters of cattle which dominate wholly or in part in crosses are the white face of the Hereford, hornlessness, and the short legs of the Dexter form in Dexter-Kerry crosses.

In horses black is dominant to chestnut and bay is dominant to either black or chestnut. Gray seems to be dominant to all other colors. In crosses of the trotter with the pacer, trotting is dominant. In swine the slaty-black, somewhat grizzled color of the wild hog is dominant to black or to red, black is dominant to red, and so-called self-white (not albino) is dominant to colored coat; "mule-foot" (uncleft hoof) is dominant to normal

foot. In the ordinary breeds of sheep white fleece is dominant to black. The occasional black sheep in a white flock is an "extracted" recessive, comparable to the red calf (Fig. 47, facing p. 134) of two black parents. Such characters as spotting and various pattern effects are usually more complicated in their unitary relation than the foregoing examples and will be better understood after a discussion of the modifications of simple Mendelism.

Terminology.—As work in the study of Mendelian inheritance progressed and expanded, the need of more precise terminology became evident and such has been gradually established. Professor Bateson coined the term "allelomorph" (Gk. *one another*, and *form*) to express more exactly what we have thus far been calling a pair of alternate or opposite characters and designated as "contrasting" or "differentiating" characters by Mendel. In the blue Andalusian fowls discussed, the white condition in the one parent is the allelomorph of the black condition in the other. The term generally means one of the pair of Mendelian characters themselves as expressed in the individual plants or animals but when the germinal basis of such phenomena is under discussion, it is sometimes used to refer to the genes of such characters. Since the visible character may vary in expression under different conditions, geneticists to-day are careful to discriminate between the expressed character and that "something" called the *factor* or *gene* which represents it in the gametes.

It is convenient also to have a brief symbol to denote a given generation and for this purpose Bateson has introduced the symbol F_1 for the hybrid progeny of the first cross, the initial letter of the word "filial." F_2 would indicate the next generation, F_3 the third and so on. Likewise P denotes the original parental generation.

It is customary where practicable to refer to the more dominating factor of an allelomorphic pair by the initial letter of the name of the character. The letter when written as a capital signifies the factor responsible for complete or partial dominance; when written as a small letter it indicates the other factor. Thus in cattle in a cross of a black animal with a red one (Fig. 47) B may be taken to represent the factors responsible for the visible condition and b the corresponding factor in the red animal. The pure-bred black animal since it has received factors for blackness from each parent, would be indicated therefore by the

letters BB, and the pure-bred red one, by bb. The black carrier of red, with one black parent and one red one, would be designated by the letters Bb. This system of nomenclature was inaugurated under the impression that the differences of allelomorphs are due to the *presence* or *absence* respectively of a particular gene. The *presence-absence* hypothesis, on account of various genetical objections—based mainly on the intermediate nature of certain hybrid characters, occasional instances of “reversed” dominance, and the not infrequent existence of a condition known as “multiple allelomorphism” in which a particular character may be the allelomorph of any one of several others—has been largely abandoned in its literal sense, although the letter system of designating allelomorphic factors has been retained by most geneticists because of its convenience. It should be borne in mind, however, that in using such formulas it is an unwarranted assumption to regard the character symbolized by the small letter as necessarily due to the absence of a gene. In some cases it seems not improbable that there is an actual absence, in others that the gene is not missing but is merely inactive or is constitutionally changed. Just as a molecule of simple sugar, for example, composed of six atoms of carbon, twelve atoms of hydrogen, and six atoms of oxygen (formula $C_6H_{12}O_6$), depending upon how these chemical elements are arranged may be any one of several very different sugars, so presumably a gene may change through intramolecular rearrangement without actually disappearing as a substance.

In pure breeds where the determiners are alike as BB in black or bb in albino guinea-pigs, the individual is said to be a *homozygote* (like things united) with reference to that character, while in those in which the determiners are unlike, as Bb, the individual is termed a *heterozygote* (unlike things united) with reference to the character. Or to use the adjective forms, a pure black guinea-pig is homozygous for pigmentation, an albino guinea-pig is homozygous for whiteness, while a cross between the two is heterozygous for pigmentation. Also, where a dominant gene is present in double quantity, that is, from both lines of ancestry, the individual is said to be *duplex*, where represented in only the single form as in heterozygous individuals, *simplex*, and where the positive factor is absent entirely, *nulliplex*, with reference to the character in question. Thus black guinea-pigs of formula BB are duplex with regard to the determiner for black

color, individuals of formula Bb are simplex with reference to this determiner, and those of formula bb are nulliplex.

Other convenient terms are *sibs* or *siblings*, to indicate all offspring of the same parents, and *propositus*, some particular individual in a genealogical system, from which a line or series of relationships is being reckoned. In modern genetics the term *hybrid* has come to be used in a much wider sense than formerly; it may refer to offspring of parents which differ in but a single pair of Mendelian characters.

Dominance Not Always Complete.—As a matter of fact close inspection shows that in numerous instances dominance is not absolute since traces of the recessive character may be detectable. For example, in the cross between smooth and bearded wheat while smoothness is regarded as the dominant character and beardedness as the recessive, nevertheless in the hybrid offspring a slight tendency toward bearding is not infrequently seen. Or again when horned breeds of cattle are crossed with hornless ones, a small proportion of such progeny will show traces of imperfect horns.

In some cases instead of either character dominating the other a form more or less intermediate between the two parents may result, as we have seen already in the case of the Andalusian fowl. Thus, certain white-flowered plants and certain red-flowered plants when crossed produce pink hybrids, and long-headed and short-headed wheats when crossed give offspring with heads of intermediate length. Or again, crosses between white and red cattle may yield red roans, and between black and white cattle, blue roans.

Thus, while for such pairs of alternative characters as have been studied, dominance to some degrees at least, seems to be the rule, still we have gradations down to the intermediate condition, and in a few known instances the hybrid with respect to a given character may be unlike either parent. The things of chief importance in the Mendelian discovery are the independent, unitary nature of the genes of hereditary characters, their segregation in the germ-cells of cross-bred forms, and their recombinations according to definite laws to form the characters of the new generation.

Modifications of Dominance.—It should be noted also that there is such a condition as *delayed dominance*. Davenport found, for example, that chicks produced by crossing pure white with

pure black Leghorn fowls are speckled black and white, but later in the adult form white becomes dominant. Likewise conditions of delayed dominance are known in man in eye-color and notably in color of hair. Some few cases have been recorded where a character is dominant at one time, recessive at another. According to Davenport extra toe in fowls may behave in this way.

Mendel's Own Work.—Mendel* himself worked out his principles on seven pairs of characters which he found in common culinary peas. These happened all to be cases in which dominance was complete. Placing the dominant character first, the pairs of characters, together with the actual numbers of each type obtained by Mendel in the F_2 generation, may be enumerated as follows:

	Individuals	Percentage
1. Tall by dwarf	787 : 277	73.96 : 26.04
2. Green pod (unripe) by yellow	428 : 152	73.79 : 26.21
3. Pod inflated by pod constricted between peas	882 : 299	74.68 : 25.32
4. Flowers along axis by flowers bunched at top	651 : 207	75.87 : 24.13
5. Seed-skin colored by seed-skin white	705 : 224	75.90 : 24.10
6. Cotyledons yellow by cotyledons green	6,022 : 2,001	75.06 : 24.94
7. Seed rounded by seed wrinkled	5,474 : 1,850	74.74 : 25.26

An inspection of this table shows that in every instance there is a close approach to a 3:1 ratio in the F_2 generation. Mendel's results have been fully corroborated by various experimenters. In the matter of yellow seed color by green seed color, for example, to mention only a few instances, Tschamak secured 3,580 yellows to 1,190 greens, Bateson, 11,902 to 3,903, and Darbishire 109,060 to 36,186.

* A translation of Mendel's original papers will be found in *Mendel's Principles of Heredity*, by W. Bateson.

CHAPTER IX

CROSSING OF INDIVIDUALS DIFFERING IN MORE THAN ONE TRAIT

Mendel found that each pair of characters followed the same law as any other pair when more than one pair of the characters occurred in the same plant, but that each pair behaved independently of the others. This makes it possible to secure various combinations of characters not associated in the original pure stocks, the number of such combinations depending on the number of pairs of allelomorphs there are.

DIHYBRIDS

Getting New Combinations of Characters.—Since this principle is well illustrated in peas, let us take two pairs of their characters, viz., greenness and yellowness (of the cotyledons) and roundness and angularity to see exactly what happens when two pairs of allelomorphs are involved. When a specific kind of yellow pea is crossed with a particular kind of green pea the offspring are always yellow (Fig. 48, opposite p. 142). When these hybrids (generation F_1) are self-fertilized, or cross-fertilized with others of the same constitution, there is the usual Mendelian segregation; one-fourth the resulting offspring will be green, one-fourth pure yellow, and one-half, although yellow in appearance, will be of the mixed type. The exact numbers found by Mendel were 6,022 yellow seeds to 2,001 green seeds. Now of the original peas (generation P) the yellow ones are round and the green ones angular (really wrinkled). Choosing this roundness and angularity respectively as a pair of characters they are found to follow the same law that the colors follow (Mendel obtained in the F_2 generation 5,474 round and 1,850 wrinkled seed), but independently of the latter. For while in the progeny of the hybrids (generation F_1), twenty-five per cent. will be round and of pure type as regards roundness, twenty-five per cent. angular, and fifty per cent. round but containing hidden factors of angularity (*i. e.*, roundness is dominant), the roundness and the yellowness, or the angularity and the greenness will not always go together as they did in the

original grandparental strains, but there will be in addition some new types of round green peas and some of angular yellow ones. That is, the factors of color and of shape have been inherited independently of one another, so that instead of the two original kinds of peas, four have been produced, viz., (1) round-yellow (one of the original types); (2) round-green (new type); (3) angular-yellow (new type); and (4) angular-green (one of the original types). Furthermore, these will be found to stand in the ratio of 9:3:3:1 respectively.

Segregations of the Genes.—How these combinations come about in this definite proportion is easily understood if the matter is expressed in terms of genes and the possible matings tabulated (Fig. 48). If we represent the gene for yellow by Y and the gene for green by y, and likewise the genes of roundness and angularity by R and r respectively, then the formulæ for the genes of these two pairs of characters in the body cells (that is, in the unreduced condition) of the pure forms and of the F₁ generation hybrids respectively are as follows:

In pure round yellow peas.....	RR YY
In pure angular green peas.....	rr yy
In the hybrid.....	Rr Yy

But now in the segregation of these genes the germ-cells of the hybrids (generation F₁) the pair of genes Rr and the pair Yy operate entirely independently of one another. Their only compulsion is that each pair be separated into the single genes, R and r in the one case and Y and y in the other. So in the separating division which brings about this divorcement R separates from r irrespective of whether it is accompanying Y or y into the resulting daughter-cell. Thus in some cases R and Y would pass into one germ-cell, in others R and y, in others r and Y, and in still others r and y, depending entirely upon the chance relations of the respective pairs to the plane of division. That is, the segregation is equally likely to be $\frac{R Y}{r y}$ giving gametes RY and ry, or $\frac{R y}{r Y}$ giving gametes Ry and rY.

Four Kinds of Gametes in Each Sex Means Sixteen Possible Combinations.—There are, therefore, with reference to the two pairs of characters under consideration, four kinds of gametes (mature germ-cells) produced in equal numbers in each hybrid, viz., RY, Ry, rY and ry. That is, in the first type

roundness and yellowness are associated, in the second roundness and greenness, in the third angularity (lack of roundness) and yellowness, and in the fourth angularity and greenness.

But since each sex has these four kinds of gametes, when they are mated there will be sixteen possible combinations. These may be tabulated as in Fig. 48, on the opposite page.

The 9:3:3:1 Ratio.—While there are sixteen possible and equally probable combinations, these will give only nine distinct kinds because some of the matings are alike. The numbers of the various kinds of matings are as follows:

(1) 1 RRYy	(4) 2 RrYY	(7) 1 rrYY
(2) 2 RRYy	(5) 4 RrYy	(8) 2 rrYy
(3) 1 RRyy	(6) 2 Rryy	(9) 1 rryy

Since roundness (R) and yellowness (Y) are dominant to angularity (r) and greenness (y) in all combinations containing R or Y, the alternative genes r or y would be obscured, with the result that individuals having certain of the combinations would look alike to our eye. For example, the individuals represented by numbers 1, 2, 4 and 5, since they contain dominant R and Y, would all appear round and yellow, although in reality No. 1 would be the only one of pure type (both elements homozygous) and hence the only one that would breed true in subsequent generations. The two individuals represented in No. 2 would breed true as regards shape (RR) but not color (Yy). Just the reverse is true of No. 4 since shape is heterozygous (Rr) and color homozygous (YY). The four individuals represented in No. 5 are heterozygous with regard to both elements. Thus nine individuals (1 plus 2 plus 2 plus 4 = 9) represented in Nos. 1, 2, 4 and 5 would be round and yellow, three individuals (Nos. 3 and 6) would be round and green, three (Nos. 7 and 8) would be angular and yellow, and only one (No. 9) would be angular and green. That is to say, the four classes discernible to the eye in generation F_2 would be present in the ratio of 9:3:3:1.

Phenotype and Genotype.—Forms such as those represented in Nos. 1, 2, 4 and 5 which to the eye appear to be alike, regardless of their germinal constitution, are said to be of the same *phenotype*. Those of the same hereditary constitution, as the two individuals represented in No. 8, or the four individuals in

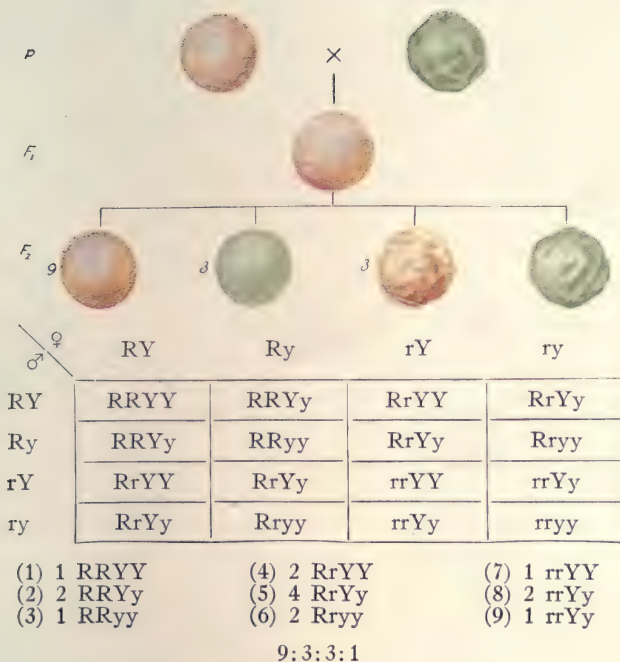


FIG. 48. Diagram showing the possible combinations arising in the second filial generation (F₂) following a cross between yellow, round (YYRR) and green, angular or wrinkled (yyrr) peas, Y, presence of factor for yellow; y, absence or inactivity of such a factor; R, presence of factor for smoothness or roundness; r, absence or inactivity of such a factor; ♂ male; ♀ female.

No. 5, are said to be of the same *genotype*, that is, they are of identical gametic constitution.

As we have seen, it is from the genotypical not the phenotypical constitution that an offspring is derived, and what a given form will bring forth depends then on its genotype.

TRIHYBRIDS

Three Pairs of Characters Illustrated in Guinea-Pigs.—Where three pairs of contrasted characters are involved the underlying principles are in no way different from those seen



FIG. 49

Diagram showing the possible combinations arising in the second filial (F_2) generation where three pairs of characters (Pigmentation X albinism, Rough coat X smooth coat, Short hair X long hair) are involved. Dominant traits are named in capitals, recessive traits, in small letters. See text and tabulation (Fig. 50) for explanation.

with two pairs of characters; the only difference is the greater number of possible combinations.

We may choose for our example the three pairs of characters used by Castle in his experiments with guinea-pigs where short hair is dominant to long hair, rough or rosetted coat to smooth coat, and pigmented coat to white coat. If for example a pigmented, long-haired, rough-coated individual is mated to an albino, short-haired, smooth-coated individual, the F_1 descendants are all pigmented, short-haired, and rough-coated (Fig. 49, p. 143). When two individuals of such parentage are interbred a series of new groupings of the characters in question appear in the next (F_2) generation. Eight phenotypes manifest themselves, five of which are unlike any of the ancestral types. Of the other three one is a complete return to one grandparent (pigmented, long, rough) in all three traits, one a similar return to the other grandparent (albino, short, smooth), and the third, like its immediate parents, shows the three dominant traits (pigmented, short, rough). In the five additional types are found the following combinations: pigmented, short, smooth; albino, short, rough; pigmented, long, smooth; albino, long, rough; albino, long, smooth. Fig. 49 represents the various matings in question and their outcome. Dominant traits are named in capitals, recessive traits, in small letters.

The various types, furthermore, are represented in the definite proportions of 27:9:9:9:3:3:3:1. The largest class manifests the three dominant characters, short, pigmented, rough coat. The smallest class exhibits the three recessive characters long, white and smooth. The three classes in the proportion of 9 each manifests two dominant and one recessive characters, and those in the proportion of 3, each display one dominant and two recessive characters. That is, all the combinations are in response to a definite law. The breeder might proceed if he chose, to fix any one of the eight types and obtain a strain which bred true to the desired combination of characters.

How these proportions come about is easily seen if the possible matings are tabulated (Fig. 50, p. 145) as was done in the case of two pairs of characters. Using the formulation P for pigmented and p for albino, S for short and s for long, R for rough coat and r for smooth coat, then, since the constitution of the original pigmented, long-haired, rough-coated guinea-pig would be represented by the formula $PPssRR$ its mature germ-

	PSR	P _s R	P _s R	P _s R	pSR	pSR	pSR	psr
PSR	PPSSRR	PPSSRr	PPSSRR	PPSSRr	PPSSRR	PPSSRr	PPSSRR	PpSsRr
PSr	PPSSRr	PPSSrr	PPSSRr	PPSSrr	PPSSRr	PPSSrr	PPSSRr	PpSsrr
P _s R	PPSsRR	PPSsRr	PPSsRR	PPSsRr	PPSsRR	PPSsRr	PPSsRR	PpssRr
P _s r	PPSsRr	PPSsrr	PPSsRr	PPSsrr	PPSsRr	PPSsrr	PPSsRr	Ppssrr
pSR	PpSSRR	PpSSRr	PpSSRR	PpSSRr	pPSSRR	pPSSRr	pPSSRR	ppSsRr
pSr	PpSSRr	PpSSrr	PpSSRr	PpSSrr	pPSSRr	pPSSrr	pPSSRr	ppSsrr
p _s R	PpSsRR	PpSsRr	PpSsRR	PpSsRr	pPssRR	pPssRr	pPssRR	ppssRr
p _s r	PpSsRr	PpSsrr	PpSsRr	PpSsrr	pPssRr	pPssrr	pPssRr	ppssrr

PHENOTYPES

PIGMENTED, SHORT, ROUGH

1 PPSSRR
 2 PPSSRr
 2 PPSsRR
 2 PpSSRR
 4 PPSsRr
 4 PpSSRR
 4 PpSSRr
 8 PpSsRr
27

albino, SHORT, smooth

1 ppSSrr
 2 pPSSrr
3

albino, long, ROUGH

1 ppssRR
 2 pPssRr
3

PIGMENTED, long, ROUGH

1 PPSSRR
 2 PPSSRr
 2 PpssRR
 4 PpssRr
9

albino, SHORT, ROUGH

1 ppSSRR
 2 pPSSRr
 2 pPssRR
 4 pPssRr
9

PIGMENTED, long, smooth

1 PPssrr
 2 Ppssrr
3

PIGMENTED, SHORT, smooth

1 PPSSrr
 2 PpSSrr
 2 PpSSrr
 4 PpSSrr
9

albino, long, smooth

1 ppssrr

27:9:9:3:3:3:1 8 Phenotypes, 27 Genotypes. Individuals in which the paired genes are similar (PP, pp, SS, ss, RR, rr) breed true for the character in question; heterozygotes (Pp, Ss, Rr) show segregation. FIG. 50. Tabulation of the 64 possible combinations in F² from a cross of a homozygous pigmented, long-haired, rough-coated guinea-pig with an albino, short-haired, smooth-coated one. Compare with Fig. 49.

cells would all be of the formula PsR . Likewise the constitutional formula of the albino, short-haired, smooth-coated individual would be $ppSSrr$ and that of its mature gametes pSr . The constitution of their immediate offspring, therefore, must be $PpSsRr$, that is, they are pigmented, short-haired, rough-coated individuals showing all three dominant characters but heterozygous for each as regards their genotypic constitution. Since only one member of any pair of contrasted characters can be represented in each gamete and there are three pairs of characters, each gamete, as regards the features under discussion, will carry three genes, no two of which are of the same allelomorphic pair. That is, there will be eight possible arrangements of the genes and therefore eight different classes of gametes as follows: PSR , PSr , Psr , PsR , pSr , pSR , psR , psr . Inasmuch as this condition prevails in each sex, and since any one of the eight different types of gametes in the one sex has the possibility of combining with any one of the eight types from the other sex, sixty-four combinations will be possible. By tabulating this situation (Fig. 50, p. 145) in the same manner the condition was tabulated in the dihybrids we can represent all the possible matings. When this is done it is evident that in the sixty-four combinations there are eight different phenotypes differing in their numbers of individuals in the proportion of 27:9:9:9:3:3:3:1 as already described. Each phenotype would have only one individual which if mated with an individual like itself would breed true, because only one individual in each phenotype is homozygous (Fig. 50, p. 145) in all members of its genotypic constitution. The pure recessive in all three traits is, of course, always homozygous, because it contains no dominant character. It requires no further fixation but will breed true at once. The numerically greatest class, however, showing 27 individuals all of the same phenotype, contains 26 heterozygous individuals and only one that is homozygous for all three dominant traits. Since this lone individual would be indistinguishable to the eye it could only be picked out by breeding tests.

The formula given on page 104 will obviously answer as well for pairs of allelomorphic characters as for pairs of chromosomes in calculating the number of *possible* combinations and the number of constitutionally *different* combinations. Thus in the trihybrid, $n = 3$; $2^n = 8$, the number of different gametes in each sex; $(2^n)^2 = 64$, the number of possible combinations; and $3^n = 27$, the number of *different* combinations (genotypes).

WHAT OF SUBSEQUENT GENERATIONS?

With no Selection the 1:2:1 Ratio Is Maintained after Generation F_2 in Cross-Fertilizing Forms.—The question of *fixing* a phenotype brings up the whole practical problem of selection. But before entering into a discussion of selection it is well to see what conditions will prevail in generations after the F_2 if no selection is practised. For the sake of simplicity the monohybrid condition, in which only one pair of contrasted characters are concerned, is considered first. Where the two gametes come from different individuals and free-intercrossing prevails, that is, where there is no self-fertilization, the 1:2:1 ratio established in the F_2 generation remains the same throughout subsequent generations.

This may be seen clearly from the chart shown in Fig. 51,

Matings and Their Relative Frequency	Types of Progeny and Their Relative Frequency from Each of the Possible Matings		
	DD	Dd	dd
♂ ♀			
DD x DD.....	1		
DD x 2Dd.....	1	1	
DD x dd.....		1	
2Dd x DD.....	1	1	
2Dd x 2Dd.....	1	2	1
2Dd x dd.....		1	1
dd x DD.....		1	
dd x 2Dd.....		1	1
dd x dd.....			1
Relation Proportion in F_3	4	8	4
i. e.	1	2	1

FIG. 51

Tabulation showing the relative proportions of the various types in generations after the F_2 , without selection in cross-breeding forms, in a monohybrid; D , dominant; d , recessive.

above, where D represents dominant and d recessive and generation $F_2 = 1 DD : 2Dd : 1dd$.

Since males and females are equally numerous this proportion would hold for each sex. The probability that a female of a given type will mate with a male of a particular type will of

course depend on the relative numbers of males of that type; any female is more likely to mate with a *Dd* male, for instance, than with a *dd* male since there are twice as many *Dd* males. Fig. 51 shows the possible matings of an F_2 generation when left to itself together with the probabilities of what the matings will be. From the table it is evident that the proportions in F_3 remain the same as in F_2 and clearly it will continue the same in all subsequent generations.

The Same True of Dihybrid or Trihybrid Conditions.— Obviously under similar conditions the same is true in dihybrids or trihybrids, since, although two or three pairs of characters are concerned, each pair operates independently of the other as an ordinary single pair of allelomorphs. In other words, with unrestricted cross-breeding, the numerical proportions of the nine genotypes in the F_2 generation of the dihybrids, or of the twenty-seven genotypes in the F_2 generation of the trihybrid, will remain the same in subsequent generations.

Selection for Dominance in Cross-Fertilizing Species.— Using the arbitrary symbols *A* and *B* to represent dominants and *a* and *b* to represent the corresponding recessives, Fig. 52, p. 149, exemplifies the result of selecting for dominance in cross-fertilizing forms, where it is desired to combine and fix two dominant traits. In the left-hand column under "Matings" are indicated the mating of the F_1 heterozygotes, and the matings of such F_2 individuals as show both dominants. Since the number of possible combinations among the gametes of F_1 dihybrids is 16, in order to avoid fractions, 16 is taken as the number on which to base the relative proportions. The customary nine genotypes, *AABB*, *AABb*, etc., which result from an F_1 mating, are represented to the right, each, with its relative frequency just below it, at the head of a column. These genotypes are seen to be in the same proportions (1, 2, 1, 2, 4, 2, 1, 2, 1) as those established in the earlier tabulation of dihybrid peas (Fig. 48, opposite p. 142). In the left-hand column the matings of all individuals visibly displaying recessive characters are omitted since the attempt is to fix a type which breeds true to dominance, and the very appearance of a form recessive in either character shows that it does not contain the genes required. The possible combinations of the four types in each sex which display both dominants in the F_2 generation, together with their relative frequencies, are indicated in the left-hand column. The results of the various matings are

Matings.		Relative frequency of each type in the progeny of the various matings.									
F_1 , AaBb x AaBb ... I x I = I...I6*		I	2	I	2	4	2	I	2	I	I
F_2		I	I
AABB x AABB...	I x I = I	I	I
AABB x AABb...	I x 2 = 2	I	I
AABB x AaBB...	I x 2 = 2	I	I
AABB x AaBb...	I x 4 = 4	I	I
AABb x AABB...	2 x I = 2	I	I
AABb x AABb...	2 x 2 = 4	I	I
AABb x AaBB...	2 x 2 = 4	I	I
AABb x AaBb...	2 x 4 = 8	I	I
AaBB x AABB...	2 x I = 2	I	I
AaBB x AABb...	2 x 2 = 4	I	I
AaBB x AaBB...	2 x 2 = 4	I	I
AaBB x AaBb...	2 x 4 = 8	I	I
AaBb x AABB...	4 x I = 4	I	I
AaBb x AABb...	4 x 2 = 8	I	I
AaBb x AaBB...	4 x 2 = 8	I	I
AaBb x AaBb...	4 x 4 = 16	I	I
Frequency of types in F_3		I6	I6	4	I6	I6	4	4	4	4	I
Relative frequency of selected types in F_3		I	I	...	I	I

* I6 progeny assumed to avoid fractions in the table.

Fig. 52

Tabulation (after Spillman) of relative frequency of various types in the progeny of generation F_2 , with cross-fertilization and selection to the dominant type when two pairs of characters are involved. The pairs of characters are represented by A, a and B, b, respectively, the capital indicating dominance.

shown to the right, the numeral representing the relative frequency of the genotype which in each case is of the constitution indicated by the formula at the top of the column in which it is placed.

The next to the last line of the table shows that while all of the various genotypes are still represented the proportions of the individuals of each class have shifted. There are still four classes (*AABB*, *AABb*, *AaBB* and *AaBb*) which show the two dominant characters it is sought to fix, but whereas the individuals of pure *AABB* constitution represented only 1/16 of the total F_2 population and 1/9 of the individuals showing dominance in that generation, through selection this *AABB* type has been increased until in the F_3 generation it represents approximately 1/5 of the total population (really 16 out of 81) and 1/4 of the individuals (see last line of table) showing dominance in both characters and from which selection must be made for the next generation.

On a similar scheme of tabulation it would be easy though somewhat tedious to plot the matings and relative frequencies in subsequent generations in order to see how rapidly a pure homozygous dominant type (*AABB*) is approached. A percentage tabulation of how such selection for dominance works out in subsequent generations is shown in Fig. 53 where selection for

Types.	Generations.				
	2.	3.	4.	5.	6.
	<i>P. Ct.</i>	<i>P. Ct.</i>	<i>P. Ct.</i>	<i>P. Ct.</i>	<i>P. Ct.</i>
<i>YYSS</i>	6.25	19.8	31.6	41.0	48.2
<i>YYsS</i>	12.50	19.8	21.1	20.5	19.3
<i>YySS</i>	6.25	4.9	3.5	2.6	1.9
<i>YySs</i>	12.50	19.8	21.1	20.5	19.3
<i>YySs</i>	25.00	19.8	14.0	10.2	7.7
<i>Yyss</i>	12.50	4.9	2.3	1.3	0.8
<i>yySS</i>	6.25	4.9	3.5	2.6	1.9
<i>yySs</i>	12.50	4.9	2.3	1.3	0.8
<i>yyss</i>	6.25	1.2	0.4	0.2	0.1

FIG. 53.

Tabulation (after Spillman) showing types and their percentages in the descendants of *YySs*, for several generations with cross-fertilization and continued selection to type *YYSS* in corn where *Y* represents yellow, *y*, white, *S*, starchiness, and *s*, sweetness.

the two dominant characters yellowness and starchiness in corn as against the recessive whiteness and sweetness are involved. In the sixth generation it is seen that 48.2 per cent. that is, nearly half of the individuals are of doubly homozygous ($YYSS$) dominant type which will breed true. Only 0.1 per cent. or one in a thousand are "throw-backs" of the recessive type homozygous in both determiners.

The same thing is graphically represented in the diagram shown in Fig. 54, up to the tenth generation. The proportion of any type from generation to generation is represented by the width of the corresponding space opposite which it is set, the first space being between the horizontal line at the top of the diagram and the uppermost curved line. The figures below indicate generations.

It will be observed that whereas in the F_2 generations only $1/16$ of type $YYSS$ is present, by the tenth generation it has increased to about 65 per cent. of the whole progeny and that the white and the sweet types have almost wholly disappeared. The yellow starchy heterozygous types have also been largely reduced, as compared with the pure homozygous $YYSS$. By continued selection the whole crop will still further approach the limit where it is entirely homozygous for the characters under selection.

Percentage of each type in each generation indicated by length of vertical line cut off by curves.

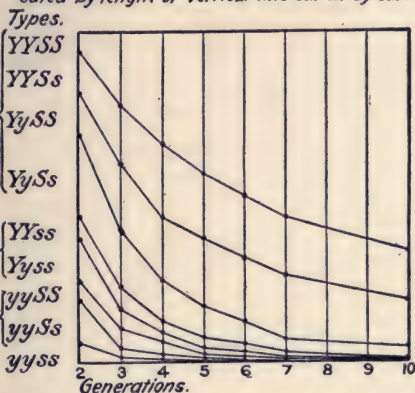


FIG. 54

Graphic illustration (after Spillman) of conditions similar to those represented in Fig. 53 carried on to the tenth generation.

Selecting for Recessives in Cross-Fertilizing Species.—Going to the opposite extreme, if one wished to select to the two recessive characters, whiteness and sweetness in the present instance, the type could be fixed from the F_3 generation on, because the very fact that both recessive traits reappeared in an individual of that generation shows that such an individual is nulliplex as regards starchiness and yellowness and consequently must be homozygous with reference to sugar and white color.

Tendency in Self-Fertilizing Species Is, without Selection, to Return to Homozygous Types.—There are many species of plants, including some of our most valuable crop plants, which are self-fertilizing or at least largely so. Among these may be mentioned wheat, oats, barley, peas and beans. The question arises what will happen to these forms if they are artificially cross-fertilized and then subsequent generations are left to themselves.

In such forms, without selection, a different result is obtained in the F_3 generation from that found in the case of cross-fertilizing species, because in the latter, any homozygote can

Types and Their Relative Frequency	Types of progeny produced by each F_2 type, and their relative frequency.		
	DD	Dd	dd
Types in F_2:			
1DD.....2*	2	---	---
2Dd.....4	1	2	1
1dd.....2	---	---	2
Frequency of types in F_3	3	2	3
Types in F_3:			
3DD.....6*	6	---	---
3Dd.....4	1	2	1
3dd.....6	---	---	6
Frequency of types in F_4	7	2	7

* Even numbers taken to avoid fractions.

FIG. 55

Tabulation (modified from Spillman) showing the relative proportions of the various types in generations after F_2 with self-fertilization and without selection, in a monohybrid; D, dominant; d, recessive.

cross back with another homozygote or with a heterozygote, but with self-fertilization a homozygote once restored remains so, since from the very fact that the plant is self-fertilizing, it can not of itself cross back with other combinations. In the progeny (F_2) of the ordinary F_1 heterozygote there would, for a single pair of dominant and recessive characters, be the usual segregation in the proportion of 1DD:2Dd:1dd, but in the production of the next generation, individuals of the DD type can only produce DD types since each gamete, male and female, which produces the new individual is from DD itself, so that

in mating there would only be $D \times D$, or DD . Likewise the dd individuals can not cross with DD or Dd as would be possible in cross-fertilizing species like corn, but must be self-fertilizing, which means they can produce only dd individuals. The Dd type being likewise self-fertilizing would break up into $1DD:2Dd:1dd$. Thus, the homozygotes always remain so and the heterozygotes always break up into $1/4$ pure dominants, $1/2$ heterozygotes, and $1/4$ recessives. There is, therefore, a steady increase in the proportion of homozygous types; they tend gradually to replace the heterozygous. The relative frequencies of these types in the third and fourth generations are indicated in Fig. 55. As is shown in the column at the

left the proportions in the F_2 generation are $1DD:1Dd:1dd$ or to avoid fractions, $2:4:2$. There will obviously be twice as many descendants from Dd parents as from either of the other types because there were twice as many Dd parents with which to start. The types of progeny produced by each F_2 type and their relative frequency are shown to the right in the chart. When all individuals of similar type are added together, it will be seen that the proportions have shifted to $3DD:2Dd:3dd$. Similarly, starting with this $3:2:3$ ration in the F_2 generation (or $6:4:6$ to avoid fractions) the relative frequency of types shifts to

$7DD:2Dd:7dd$ in the F_4 generation. Fig. 56, above, shows the result for two pairs of characters without selection in a self-fertilizing species, at the end of ten generations. The chart represents two pairs of characters in wheat: W , winter character; w , spring character; C , club character (short thick head); c , long-head character. All individuals of similar appearance and habits

Lengths of vertical lines cut off by curves show proportion of types in each generation.

Types.

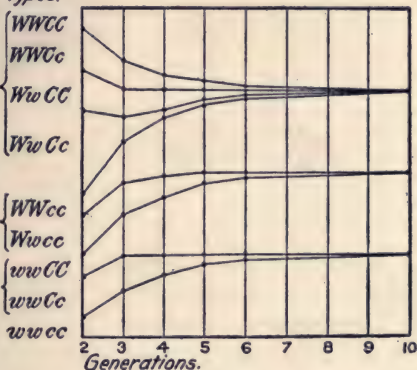


FIG. 56

Graphic illustration (after Spillman) of ten generations of a hybrid in a self-fertilizing species (wheat) without selection to type: W , winter character; w , spring character; C , club character; c , long-head character. The population ultimately comes to consist almost entirely of the four homozygotes.

(similar phenotypes) are grouped. The space opposite each formula shows the proportion of the type represented by that formula.

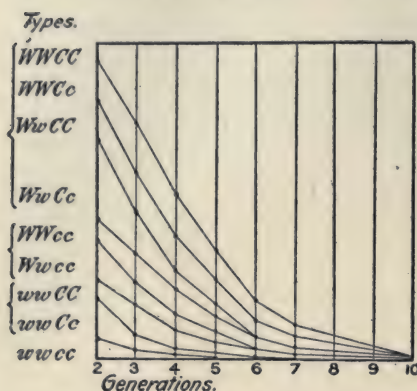


FIG. 57

Graphic illustration (after Spillman) of mass selection in wheat, a self-fertilizing species, for types $WWCC$. The letters and spaces have the same significance as in Fig. 56.

for winter club wheat is shown in Fig. 57, above. It is seen that the homozygous $WWCC$ type has almost completely supplanted the others. With self-fertilizing plants, however, it is possible to practise *individual selection* instead of mass selection and thereby quickly fix a type. This is indicated in Fig. 58, p. 151. In individual selection each plant of the F_2 and subsequent generations is kept to itself. Since it is self-fertilizing it reveals its own gametic constitution in the next generation; if heterozygous it breaks up into the expected

la. It is obvious that by the tenth generation the population comes to consist wholly of the four homozygous types; viz. $WWCC$, $WWcc$, $wwCC$, $wwcc$.

Selecting for Dominance in Self-Fertilizing Species.

—If *mass selection* is practised, that is, if all phenotypes that show both dominant characters are selected each time, both homozygous and heterozygous forms will appear in the next generation, but heterozygotes will become proportionately less in each succeeding generation. The result of such mass selection at the end of ten generations

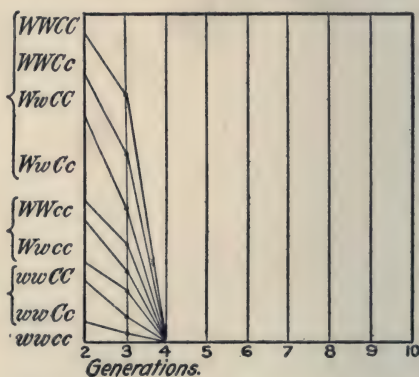


FIG. 58

Graphic illustration (after Spillman) of the effect of individual selection in a self-fertilizing species (wheat) on progeny of the hybrid ($WwCc$). The letters and spaces have the same significance as in Fig. 53.

ratio for simplex types, if homozygous it breeds true. The problem of getting a desired type through selection, therefore, where individual selection can be practised, as with self-fertilizing plants, becomes much simpler than with cross-fertilizing species, unless the latter are plants which can be artificially self-fertilized.

CHAPTER X

MORE COMPLEX MENDELIAN PHENOMENA

Often a number of genes, independently inheritable, are involved in the production of a visible character. Not infrequently what at first sight appears to be a pair of allelomorphs is in reality not so. Or it may be that a given character, such as color, may be produced by any of several independent determiners. It is evident that through such conditions confusing complications of the simple Mendelian ratios are likely to arise. So many examples of factorial interaction are now known, indeed, that present-day geneticists are inclined to regard each gene as probably influencing more or less profoundly many others. It has become clear that any particular part of an individual, even though shown by breeding tests to act as a unit-character, must necessarily, when considered in its entirety, be the resultant of a number of cooperating factors, hence a unitary difference as studied in genetics is probably the result of a *factor difference* among these several components rather than of a lack of all the constituents which are required to make up the expressed character. The developing organism is in fact an intricate reaction system and any "character" in its finished form may be the product of the whole germinal complex. Add or subtract any one of a multitude of *modifiers* and the outcome will be different.

Supplementary Factors.—The inheritance of form of comb in fowls as described by Bateson and Punnett, is a good illustration of a condition which is somewhat more complicated than those considered so far but which when understood is readily resolvable to Mendelian formulation. Such cases, which involve interaction of factors belonging to different allelomorphic systems, are of particular interest since it seems highly probable that many compound characters exist which will become intelligible only upon similar painstaking disentanglement of the related elemental factors.

Four types of comb are involved in the cases to be discussed, namely:

1. *Single comb* (Fig. 59a, below), a high, single, toothed plate such as is commonly seen in the Leghorn.
2. *Rose comb* (Fig. 59b), a broad comb with its upper surface covered with papillæ and provided with a backward projecting pike, characteristic of Hamburgs.
3. *Pea comb* (Fig. 59c), a comb such as is seen in Indian games, consisting of three parallel ridges—a prominent central and two less conspicuous laterals.
4. *Walnut comb* (Fig. 59d), a comb dimpled in at the sides, having a fanciful resemblance to a half walnut, seen normally in the Malay fowl.

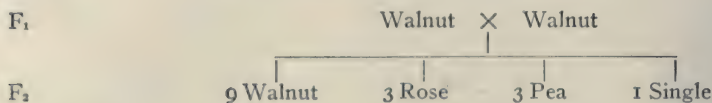


FIG. 59

Diagram showing comb character in fowls (modified from Punnett):
a, single; b, rose; c, pea; d, walnut.

When rose- and single-combed forms are crossed rose is dominant. When pea- and single-combed forms are crossed pea is dominant. But when rose- and pea-combed forms are crossed neither form of comb appears as a dominant, but a new type, walnut (Fig. 59d) is produced.

When walnut-combed individuals of the F_1 generation produced by crossing rose- and pea-combed forms respectively are bred together all four types of comb are produced and in the ratio of 9:3:3:1 as follows:



From the numerical proportions it is evident that the formula is the same as where two pairs of allelomorphic characters are concerned (Fig. 48, facing p. 142). Rose and pea are obviously not allelomorphs one of another. If the gene for rose be represented by R and its corresponding recessive by r, and that for pea by P and its recessive by p, then the zygotic constitution for rose may be written RRpp and the gametic Rp (that is one deter-

	RP	Rp	rP	rp
RP	RRPP Walnut	RRPp Walnut	RrPP Walnut	RrPp Walnut
Rp	RRPp Walnut	RRpp Rose	RrPp Walnut	Rrpp Rose
rP	RrPP Walnut	RrPp Walnut	rrPP Pea	rrPp Pea
rp	RrPp Walnut	Rrpp Rose	rrPp Pea	rrpp Single

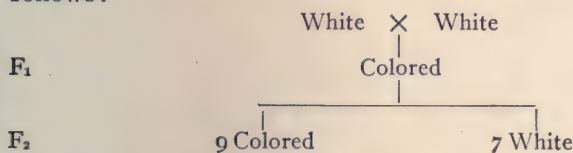
FIG. 60

Tabulation of the F_2 generation produced from walnut-combed fowls of constitution RrPp.

miner for rose and the other for the absence of inactivity of pea). Likewise the zygotic constitution for Pea is rrPP and the gametic is rP. When Rose and Pea are crossed, then $Rp \times rP = RrPp$, a heterozygote which is expressed as the walnut type. Since this type is dihybrid, it produces the four equal classes of germ cells, RP, Rp, rP and rp. Each sex will have the four classes of gametes and therefore sixteen combinations are possible (Fig. 60, above), resulting in the production of nine genotypes and four phenotypes, the latter in the familiar 9:3:3:1 ratio. That is, in the F_2 generation (Fig. 60), counting on the basis of 16 fowls, 9 should contain the factors for both rose

and pea, 3 the factor for rose but not for pea, 3 the factor for pea but not for rose, and 1 neither the factor for pea nor rose. The last type gives single comb. Rose-comb, then, may be regarded as single-comb modified by a factor which makes it rose, and pea-comb, as single-comb modified by a factor which turns it into pea. When both of these modifying factors are operative in the same individual what would otherwise have been single-comb becomes walnut. When a given character represented by a particular factor is thus modified by the introduction of a different factor, the latter is termed a *supplementary factor*.

Complimentary Factors Illustrated by the 9:7 Ratio.—As a further example of characters which depend upon more than one factor in the zygote we may take the condition found in certain sweet peas. The ordinary varieties of white sweet peas when left to themselves breed true to whiteness. Bateson and Punnett found, however, that when certain strains of whites were crossed they produced colored flowers. These in turn when interbred yield colored and whites in the proportion of 9:7 as follows:



The conditions are most readily interpreted on the supposition that two separate independently inheritable chemical substances, which may be designated as color base and color developer, combine to produce color. If either or both are absent, the flower will be uncolored. If we designate the one substance by A and the other by B, then the constitution of the one white sweet pea for color may be represented by the formula AAbb and the other by aaBB. That is, one strain may be thought of as having lost the A factor and the other strain the B factor sometime in its ancestry. The gametes would be respectively therefore Ab and aB, and the zygotes or individuals of the F_1 generation resulting from the union of such gametes would have the constitution AaBb. Since here A and B are together in the same individual the color must appear. It is obvious from the formula that the case is simply one of an ordinary dihybrid as already analyzed in Fig. 48, facing p. 142, for two pairs of characters.

The gametes of the F_1 colored individuals will form the conventional four classes in each sex; namely, AB, Ab, aB, ab, and the matings may be tabulated in the usual form, (Fig. 61, below).

An examination of this table shows that of the 16 possible combinations 9 have at least one A and one B together and 7 do not. And since the union of A and B means the production of color and their existence apart means white, 9 will yield colored flowers and 7, white ones. Such separately inheritable, dissimilar factors, the combination of which is necessary for the production of a particular character, are called *complimentary factors*.

To be sure that one understands the situation, it is well to work out in complete tabular form such problems as the following: What is the result of breeding together: (a) two plants of

	AB	Ab	aB	ab
AB	AABB Colored	AABb Colored	AaBB Colored	AaBb Colored
Ab	AABb Colored	AAbb White	AaBb Colored	Aabb White
aB	AaBB Colored	AaBb Colored	aaBB White	aaBb White
ab	AaBb Colored	Aabb White	aaBb White	aabb White

FIG. 61

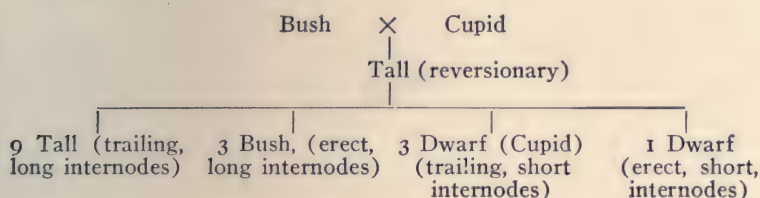
Tabulation of the F_2 generation produced from heterozygous colored sweet peas of genotype AaBb where both factors A and B are necessary for the production of color; the 9:7 ratio.

formula AABB? (b) a white of constitution aabb and any other white? (c) a white of constitution Aabb and one of constitution aaBb? The answers should be: (a) three-fourths of the progeny colored and one-fourth white; (b) all white; and (c) one-fourth colored and three-fourths white.

Reversion Explained on a Mendelian Basis.—Many cases of *reversion* are explicable on the supposition that in crossing two strains, complimentary factors are united again which had somehow become separated in past generations of the strains

in question. This is true not only of color but of other features as well. A good example of a reversion in structural characters as well as color is seen when the Cupid sweet pea and the Bush sweet pea are crossed. The Cupid is a dwarf variety distinguished by very short internodes (distance between leaves) and trailing habit. The Bush sweet pea on the contrary has long internodes and an upright habit of growth which gives it the appearance of a compact bush. When Bush and Cupid varieties are crossed the F_1 generation plants show a *reversion* to the tall size and trailing habit of the wild Sicilian sweet pea from which all cultivated varieties are believed to have been derived originally.

The progeny of such reversionary individuals appear as four types in the ratio 9:3:3:1 as follows:



The ratio is clearly the simple Mendelian proportion which occurs when two pairs of allelomorphs are involved. The characters concerned are: (1) long internode (dominant) X short internode; and (2) trailing habit (dominant) X erect habit. As regards habit of growth and length of internode the Cupid variety would seem therefore to be a wild type lacking the factor for long internodes, and the Bush, a wild one minus the factor for procumbent or trailing habit of growth. The new erect dwarf secured is apparently one without either of these factors.

Other well-known cases of reversion are probably to be similarly interpreted in Mendelian terms, such as the reverting in pigeons to the wild blue rock type (*Columbia livia*) with black wing-bars or with black-checked wings, when certain domesticated races of pigeons are cross-bred; or the return to the black-and-red coloration of the wild jungle fowl when certain breeds of fowls are crossed. A notable example of the latter is that secured by Bateson and Punnett in the F_1 generation from a cross of two white types; namely, a recessive white hen by a white silk cock. Apparently the colors in the F_1 fowls are produced by bringing together complimentary factors from the

two white types. Similarly crosses between two varieties of white rabbits (not albinos) may produce all gray young like the wild type.

Probable Origin of Certain Varieties of the Cultivated Sweet Pea.—One of the best known examples of the interaction of factors where several factors modify the same character is found in a cross of the sweet pea (*Lathyrus odoratus*). In this case a complete reversion to the purple color of the wild Sicilian form was secured by crossing two white varieties of sweet pea. In Fig. 62, opposite, 1 and 2 represent the parent types and 3 the *reversionary* purple in question. Subsequent breedings from this purple type showed that at least 5 factors are concerned in its production. Its immediate progeny appeared as colored forms and whites in the ratio of 9:7, as already described (p. 159), but among the colored ones there were 6 distinct types. Of these 3 showed purple (Fig. 62, 4, 5, 6) and 3 were red without any purple (7, 8, 9). The purples were respectively, the original wild Sicilian bicolor type with blue wings (No. 4), a deep purple type with purple wings (5), and finally a much lighter purple type (6). The three corresponding reds included a bicolor red with pinkish wings (7), a red with red wings (8), and very pale red or tinged white (9).

After exhaustive experiments necessitating the breeding of many thousands of plants it was found that at least five color factors were involved, enumerated by Punnett as follows: R, a color base; C, a color developer; B, a blue factor; L, a light-wing factor; I, a factor for intense color. The formulæ for the several forms, without using double characters and entering into whether a given colored individual is homozygous or heterozygous, are as follows:

Purples

1. Purple bicolor (No. 4 of Fig. 62) C R B L I
2. Deep purple (No. 5).....C R B l I
3. Light purple (No. 6).....C R B L i or C R B l i

Reds

4. Red bicolor (No. 7).....C R b L I
5. Deep red (No. 8).....C R b l I
6. Tinged white (No. 9).....C R b L i or C R b l i

It will be observed that the reds differ from the purples in not possessing the blue factor, B. With B present they would



FIG. 62. Drawn and colored from a plate by Punnett. Two white strains, 1 and 2, when crossed produce a reversionary bicolor purple with blue wings; 4, 5 and 6, correspond to 7, 8 and 9, respectively, with a "blue" factor added.

all be turned into corresponding purples. Actual breeding showed purple dominant to red inasmuch as in the F_2 generation there were three purples to every red, the simple Mendelian ratio for a single pair of characters. The remaining factors were established from the proportions in which the three classes of purples appeared, viz., 9 bicolors, 3 deep purples and 4 (3 plus 1) light purples. According to Punnett's interpretation the presence or absence of two factors—(1) a factor I for intense color (present in the bicolor and deep purple forms, absent in the dilute purple), and (2) a light-wing factor L, which when present renders its possessor dominant to the dark-winged form—would account for all the observed modifications, hence these factors were inferred to exist.

Another interesting fact about these color types is that some of them are apparently the same as certain known cultivated varieties of sweet peas. Thus according to Punnett the bicolor purple with blue wings is apparently the Purple Invincible; the dilute purple, the Picotee; the bicolor red, the Painted Lady; the deep red, the Miss Hunt.

It becomes a very plausible hypothesis to suppose, therefore, that the various cultivated forms of the sweet pea have arisen from the wild Sicilian purple, by the loss or change of one or more of the factors which exist as a complete set in this ancestral wild form. This again, together with other similar evidence suggests that perhaps many of the varieties of cultivated plants or domesticated animals may have arisen in the same way through loss or change of one or more factors present in the original wild form.

From the foregoing examples it is plain that there are characters which require more than a single kind of determiner to bring them to expression. Conversely it is evident that a single determiner, for example the factor I in the last illustration, may influence more than one character. Some of the cases become highly complex and one can but marvel at the remarkable analyses which have been accomplished through the ingenuity and patience of experimental breeders. According to Professor Erwin Baur twenty or more factors are involved in determining the color and form of flowers in *Antirrhinum*, the snapdragon. The interaction of at least seven factors and probably of many more, are required for the production of the simple coat pattern visible in wild house mice, and more than a dozen factors are

known which affect the color of the common corn plant. As the characters of plants and animals are more and more carefully and extensively analyzed, indeed, it becomes apparent that a given character is the expression of the finely balanced interactions of many factors.

Coat Color in Mice (the 9:3:4 Ratio).—Another instructive example of factorial interaction and “reversion” has been found in cross-breeding certain varieties of “fancy” mice. The grayish-brown or grizzled coat of the ordinary wild mouse is supposedly the original ancestral coat color. Such an inconspicuous coat, often cited as an example of “protective coloration,” is known as the *agouti* pattern, and is found in many wild rodents such as squirrels, rabbits, various species of mice and rats and many others. The individual hairs which make up the pattern in such animals are mostly black with a narrow yellow band near the tip. Both yellow and black pigments are present in the agouti pattern, absence of the yellow pigment leaves an individual with solid black fur. Such black breeds true but is recessive to the wild gray type. Albinos are white, pink-eyed individuals devoid of pigment or showing only traces of it. Albinos breed true when mated together but albinism is recessive to any color.

When black mice are crossed with albinos the offspring are usually all agouti; or in other words, there is a color reversion to the wild type. When such F_1 agoutis are interbred, however, their progeny show, on the average, a ratio of 9 agouti: 3 black: 4 white. The result is explicable on the assumption that for the production of color a factor C is present, and for the yellow-banding of the black hairs which produces the agouti pattern, an additional factor A is necessary. Black mice contain the factor C but not A . Albinos lack the factor C . In the crosses under consideration, however, albino parents must carry the factor A . Its presence is not realized because in the absence of pigment (factor C) its effect can not become visible. Thus supposing the original black parent is represented by the formula $CCaa$ and the albino parent by $ccAA$ then the F_1 agouti will be represented by the formula $CcAa$. The expected composition of the F_2 progeny of two such F_1 agoutis is tabulated in Fig. 63, p. 165. Wherever both A and C occur in the same individual the agouti pattern appears; when C occurs alone the animal is black; and where C is absent with A either present or absent, the individual is albino.

A similar 9:3:4 dihybrid F_2 ratio was observed by Castle in guinea-pigs when blacks were crossed with red ones which transmitted the agouti (A) factor.

From the foregoing modified dihybrid F_2 ratios it becomes apparent that if neither of the two factors involved in a cross can produce a visible result in the absence of the other the ordinary F_2 9:3:3:1 ratio becomes 9:7, since the last three classes all look alike. If on the other hand one of the two factors involved can produce a visible effect but the other can not, except in the presence of the first, then the F_2 ratio is modified to 9:3:4 because only the last two classes are indistinguishable.

Many Interrelated Factors in the Production of Rodent

	CA	Ca	cA	ca
CA	CCAA Agouti	CCAa Agouti	CcAA Agouti	CcAa Agouti
Ca	CCAa Agouti	CCaa Black	CcAa Agouti	Ccaa Black
cA	CcAA Agouti	CcAa Agouti	ccAA Albino	ccAa Albino
ca	CcAa Agouti	Ccaa Black	ccAa Albino	ccaa Albino

FIG 63

The 9:3:4 ratio in the F_2 generation from a cross of black by albino mice which produced all agouti animals (reversionary wild type) in the F_1 .

Coat Colors.—As a matter of fact careful genetic analysis has shown that in the various color varieties of rabbits, mice and other rodents known to fanciers, a number of interrelated factors are concerned. According to Castle the gray coat of a rabbit depends upon at least five different genes; namely (1) a color factor necessary for the production of any color; (2) a black factor; (3) an extension factor; (4) an agouti factor; (5) an intensity factor. The color varieties of gray, black, yellow and white rabbits are all the result of various combinations of the different forms of these five genes. The fact that there

are 32 different genotypes of similar-looking gray rabbits known shows how complex the formulation may become.

In the coat colors of mice at least a dozen such factors, all of which segregate distinctly and which may occur in any combination, have been worked out. Thus C is a color factor without which there can be no pigmentation. B is responsible for the development of black pigment; it is dominant over b which represents brown or chocolate, A is the agouti factor. S determines *self*, that is solid color as against s which signifies white, spotted or piebald coat. P indicates normal, intense eye-color as against a recessive pink-eyed condition (p) which is also accompanied by a faded appearance of the fur caused by a reduction in the amount of the black and brown pigment. The fully-pigmented condition, D, has as its recessive a factor d (dilute) which causes a clumping of the black or brown pigment granules in the hairs and makes the colors appear faded. Thus for the production of the agouti pattern and coat color of the wild mouse there must be interaction of at least the factors, A, B, C, D, P, and S in either heterozygous or homozygous condition, and probably also of many other factors.

In spotted mice there is at least one distinct factor for white spotting. Spotted coat is recessive to self-colored coat. The degree of spotting may range from a small white area on an almost self-colored coat to a coat which is more than half white. Different amounts of spotting, however, may be inherited. This is due presumably to *modifying factors* which influence pigment production. Although these factors may be present in either albino or self-colored mice in independently heritable form, they can only become visibly expressed in the presence of factors for white spotting. Many other examples of such modifying factors, which affect the degree of development of a particular character, are known in both plant and animal genetics. In the fruit fly at least fifty genes are known to cooperate to produce the characteristic red color of the eye, and seven factors have been identified in this form which produce a quantitative effect on white eye color, itself the result of a single factor.

There is also a dominant factor for yellow present in some mice, but it appears only in the heterozygous condition, and yellow mice, therefore, like blue Andalusian fowls or roan cattle will not breed true. Apparently the combination of two yellow-bearing gametes produces a zygote which is non-viable, so that

no individuals of constitution YY are born. This, at least, is the only explanation forthcoming for the fact that matings between two yellows produce two yellow offspring to one non-yellow instead of the 3:1 ratio expected from monohybrid heterozygotes. The duplex (YY) type is missing. There is evidence that all three classes (YY, Yy and yy) are formed but that the homozygous yellows (YY) die as embryos.

Lethal Factors.—Factors such as the ones just mentioned which cause the early death of the zygote or in some cases of gametes, are called *lethal* factors. They are known among both plants and animals. Morgan and his associates have discovered about forty distinct lethal factors in *Drosophila* alone. Obviously only heterozygous individuals, in which the lethal factor is balanced by a normal one, can survive. The condition is detected by the way in which the expected Mendelian ratio is modified. The class of offspring that would be represented by the homozygous condition of the lethal is lacking. A good illustration of lethal factors is found in various albino plants notably corn and sorghum. Chlorophyl, the green coloring matter of green plants, is required in the manufacture of the plant's food, hence young white or albino plants soon die. Plants are found occasionally, the self-fertilized seeds from which produce green seedlings and white seedlings in the proportion of 3 to 1, the simple Mendelian ratio. Such parent plants are evidently heterozygous for a factor that results in absence of chlorophyl. In the heterozygotes since the condition is balanced by a normal factor no harm results but in such offspring as inherit both factors for white, death must follow because of lack of capacity to carry on normal nutritive processes.

Epistasis.—It sometimes happens that a factor conceals or prevents the expression of another which is not its allelomorph. Such masking of one factor by another is known as *epistasis*. The overshadowing factor is said to be epistatic to the other; the latter is said to be hypostatic. Epistasis is well exemplified in the epistatic series of six grades in the decreasing amount of black in relation to blue described by Miss Jones in her study of the inheritance of checks and bars in pigeons (Fig. 64, p. 168). The several grades named in the order of their epistatic manifestation with reference to those which follow were (1) Full black, (2) Black, blue-tail, (3) Checked, (4) Sooty, (5) Blue black-barred, and (6) Blue barless. Each grade (disregarding

Epistatic Series in Pigeons



S — Black



sT — Black blue-tail



st C — Black check



stc So — Sooty



stc so Ba — Blue black barred



stc so ba Blue barless

FIG. 64

Six distinguishable grades of the epistatic series showing the successive decrease in the amount of black (spread pigment) in relation to blue (clumped pigment) in the pigeon; S, black due to even spreading of pigment granules; s, blue due to clumped condition of pigment granules; T, black blue-tail; C, check; So, sooty; Ba, barred; the corresponding small letters indicate recessive condition (from Jones: *Publication Wisconsin Agricultural Station*, No. 30.)

minor variations in pattern) was shown by breeding tests to be genetically distinct. Any particular grade was found to be epistatic to each or all others below it. Miss Jones found that the same patterns were also distinguishable in the so-called dilute series of coloration, namely: full-duns, dun silver-tails, dun checks, sootied silver, silver with dun wing-bars, and (probably) silver barless.

An interesting example of epistasis in poultry is seen in the almost complete dominance of the white of White Leghorn fowls over the colored plumage of various colored varieties. The white plumage of such breeds as white Plymouth Rocks or

	CI	Ci	cI	ci
CI	CCII White	CCII White	CcII White	CcII White
Ci	CCII White	CCii Colored	CcII White	Ccii Colored
cI	CcII White	Ccli White	ccII White	ccII White
ci	Ccli White	Ccii Colored	ccII White	ccii

FIG. 65

The 13:3 ratio of the F_2 generation from a cross of a breed of fowls (White Leghorn) with dominant white plumage by one with recessive white plumage; C , factor for color; I , color inhibitor.

White Wyandottes seems, like albinism, to be due to lack of some necessary color factor, and as in true albinos, it is recessive to colored plumage. The dominant white of Leghorns, however, results from the presence of a factor which inhibits or prevents the development of color in the plumage, even though, as may be proved by suitable breeding tests, White Leghorns actually contain a color factor. If the color factor be denoted by C , and the inhibiting factor by I , then the constitution of the White Leghorns in this respect is $CCII$, while that of such a breed as the Wyandottes is $ccii$. The F_1 progeny from a cross between

these two strains would be whites of constitution $CcIi$, and the F_2 offspring should show, as may be seen readily if the possible F_1 combinations are drawn up in the usual checkerboard form (Fig. 65, p. 169), thirteen whites (or whites with dark backs) to three colored. In other words the I factor will be present in twelve of the combinations, both I and C will be absent in one, and C unaccompanied by I will be present in only three. Actual breeding results are in close agreement with this expectation.

Multiple Effects of a Single Factor.—Not only is a single visible character often due to the operation of many factors, but conversely a single factor may affect many different characters. So that, while it is customary to refer each detectable character-difference to a particular gene, the fact that this same gene may also have a part, possibly even a more important one, in the expression of one or more other traits must not be overlooked. Numerous instances of such manifold effects are known. Mendel himself observed that when a certain pigment-developing factor was present in his plants that not only were the flowers purple but reddish spots appeared in the axils of the leaves and the seeds bore brown or gray seed coats. Such varied local expressions of a single fundamental germinal difference have been recorded for many other plants. In the fruit fly, *Drosophila*, Müller has shown that a single factor is concerned with such diverse characteristics as length and shape of wings, abnormally shaped abdomen, characteristic disarrangement of bristles, infertility and viability. Many more examples might be cited which indicate that each gene, although a unit in itself, probably exerts influence on many parts of the organism.

Environmental Modifications of Factor Expression.—Not only is an organism formed under the cooperative influence of specific genetic factors but it is also measurably conditioned or modified by the environment—external or internal—under which these factors become expressed. In the chapter on the mechanics of development (Chapter V) attention has already been called to the profound effects which changes in the external conditions may bring about in a developing or regenerating organism. From such facts it is evident that the same set of genes may produce different results under different conditions. As further exemplification some of the modifications which appear in the fruit

fly, *Drosophila*, under changed environment, may be cited. Certain fruit flies, when reared in the cold, tend to produce supernumerary legs and the condition is inherited in the Mendelian manner in these particular stocks as long as the temperature is kept low. When kept properly warmed, however, even though they carry the genes responsible for such deformities, the offspring are normal. Likewise a certain factor in *Drosophila* known as "bent," which under ordinary conditions results in a characteristic change in the wings and in a shortened, twisted condition of the legs, also induces, when "bent" flies are reared in a cold atmosphere, characteristic irregularities in the compound eyes, in the veining of the wings and in the bristle arrangement on the thorax. Again fruit flies of the same genetic constitution can be made to show a reduced number of facets in the compound eye by a change of temperature. On the other hand individuals with few facets appear from time to time under ordinary temperature conditions and produce offspring, in the Mendelian manner, with few facets. Thus the same visible modification is due in one case to environment, in the other to heredity. Many similar facts might be cited among other organisms. The only sure way of distinguishing between hereditary and environmental factors is through experimental breeding.

The interdependence of genetic factors and internal environmental agencies has already been exemplified in the discussion of hormones (p. 78), where it was observed that many characteristics of higher animals require the cooperation of these internal secretions for their expression. By way of further illustration the peculiar "hen-feathering" of the males in certain breeds of fowls such as the Sebright bantams, may be cited. In such breeds a dominant factor for hen-feathering occurs which is transmissible through both males and females. Morgan found that if such hen-feathered males have the sex glands removed they assume typical male plumage. Hen feathering in the male, therefore, requires the presence of an internal secretion from the testis for its expression. Most if not all of the secondary sexual differences in vertebrates, in fact, require for their normal development not only an inherited foundation but also the cooperation of sex hormones.

An interesting example of the influence of sex upon dominance is found in the inheritance of horns in sheep. When, for example, a breed like the Dorset which is horned in both sexes

is crossed with a hornless breed such as the Suffolk, the male offspring are all horned and the females all hornless. This is true irrespective of whether it was the male or the female parent which was horned. Evidently a single factor for horns is sufficient in the male heterozygote to cause the development of horns but insufficient in the female. When two such heterozygotes are bred together, however, about three-fourths of the male offspring are horned and one-fourth hornless, while only one-fourth of the female offspring are horned and three-fourths are hornless. In other words in the 1:2:1 ratio of the F_2 generation the males of duplex and those of simplex constitution display horns while those of nulliplex constitution are hornless. On the other hand only females of duplex constitution develop horns. Apparently in the male heterozygote the single factor for horns when reinforced by the internal secretion from the sex gland is sufficient for horn formation. A similar sex limitation for baldness in man was found by Dorothy Osborn in observations on twenty-two families in which baldness occurred. She found that baldness acts as a dominant from father to son but as a recessive in woman since it appears in woman only when present in the duplex (homozygous) condition.

Inbreeding and Outbreeding.—To any form of breeding which involves the mating of relatives the term *inbreeding* is applied. Since all members of a particular "breed" are related in some degree the term is ordinarily restricted to matings between parent and offspring, brother and sister, cousin and cousin or to other individuals showing similar close relationship. Matings between distantly-related or unrelated individuals constitute *outbreeding*. The term *cross-breeding* is often used interchangeably with *outbreeding* although some restrict it to the mating of plants or animals of different varieties or breeds.

In establishing breeds or pedigreed strains of live stock generally inbreeding has been practised to a marked degree. The result has been the production of uniform and valuable types as is evidenced by any of our popular breeds of cattle, sheep, hogs or horses, or by many of our varieties of crop plants. Although what the practical breeder has accomplished could not have been gained without the aid of inbreeding there is a wide-spread opinion that the effect of inbreeding on progeny is pernicious. That inbreeding *per se* is not surely harmful is

clearly indicated by the fact that such successful plants as oats, peas and beans are naturally self-fertilizing, thus exhibiting the most intense form of inbreeding. On the other hand, as shown by Shull, East, Jones and others, corn, a naturally cross-fertilizing plant, deteriorates during the first few generations of inbreeding, although after seven or eight generations it tends to remain stable, without further decrease in size of plant or yield.

While the evidence is somewhat conflicting and there is still a shortage of data from carefully controlled experiments it seems that indiscriminate inbreeding, without selection for strength or fertility, leads ordinarily to decline of vigor, increase of death-rate, sterility and even sometimes deformity in many animals, and to loss of yield and other evidences of deterioration in various plants, while on the other hand, if all enfeebled, infertile and unpromising individuals are weeded out generation after generation, and only vigorous productive individuals are selected for breeding, the strain may be improved and made more uniform.

The careful work of Miss King at the Wistar Institute, and of Sewall Wright, under the auspices of the United State Department of Agriculture, are two outstanding investigations in this field. Starting with four normal though rather undersized albino Norway rats, two males and two females, Miss King made brother and sister matings for a number of generations. No selection was practised for the first six generations during which time the inbred rats showed decline in fertility and other evidence of enfeeblement. However, it is not clear that this decline was not due to a deficiency in the food, for non-inbred members of the rat colony also showed similar changes during the same period. On an improved ration both inbred and stock rats improved in growth and fertility, and no further decrease in vigor occurred in the inbred animals. After the sixth generation some twenty superior females from about a thousand were selected and thereafter for twenty-five generations only the most vigorous animals were used for breeding purposes. In this way Dr. King established what was essentially a homozygous race of rats superior in many ways to the stock from which they originated. Apparently, through selection, all undesirable characters had been culled out, and a standard, healthy race established. Dr. King's results are based on a total production of about 25,000 young.

Dr. Wright's experiments involved a maximum of twenty-three generations of brother-sister matings and records on some 30,000 animals, during the period 1906 to 1922. He used a number of different families and therefore could make comparisons between family strains and the results of crossing different families, as well as observations upon the effects of inbreeding on particular traits in a given strain. He also used outbred controls. Wright did not select only the best for breeding purposes, consequently his experiments probably approximate what would happen under natural conditions. In general he found the result of continued inbreeding in guinea-pigs to be a steady loss in all elements of vigor. The size and number of litters declined; resistance to tuberculosis diminished; and both weight and growth-rate were adversely affected. Some strains declined so rapidly that they became extinct in a few generations; others remained strong after long inbreeding. Decline of vigor took place in different ways in different families. Wright found that decided differences among families were brought to light and fixed by inbreeding, including tendencies toward the appearance of particular types of abnormalities. Various elements of vigor proved to be inherited independently of each other. In his own words, "Each family has come to be characterized by a particular combination of traits usually involving strength in some respects with weakness in others." Inbreeding experiments with swine and poultry agree in general with Wright's results on guinea-pigs.

As far as present data warrant a conclusion the upshot of the whole matter seems to be that inbreeding tends to establish homozygous strains. If the inbred individuals possess many undesirable characters these are concentrated in the stock. In particular, harmful recessives are brought to the surface and, uncompensated by a normal dominant, they work havoc. In brief it is not inbreeding itself but a masked poor heredity which is to blame. By inbreeding, it is evident that unfavorable recessive characters may be brought to light and weeded out of a stock. This has probably been done automatically by natural selection in self-fertilizing plants. Sexual reproduction, where the sexes are separate, is essentially a hybridizing mechanism, and one can see how harmful recessives might become widely disseminated through a stock when overshadowed by neutral or favorable dominants, and how they can be revealed by anything tending to produce homozygosis.

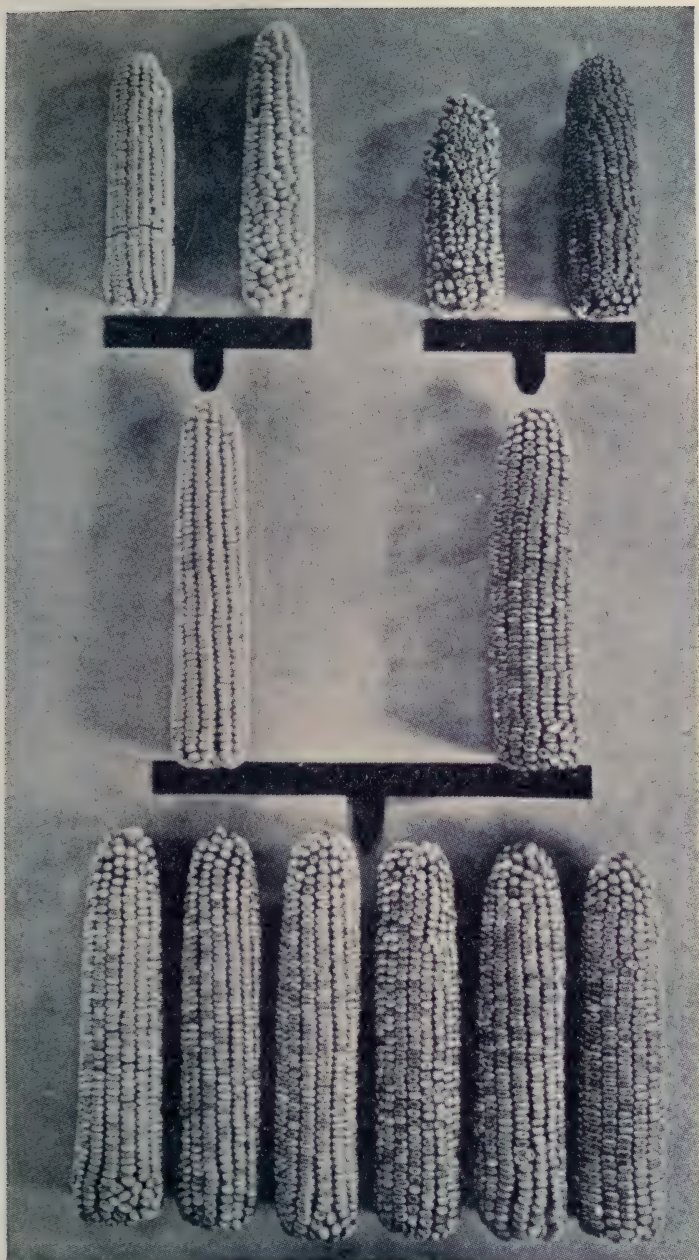


FIG. 66. Heterosis in corn and the effects of double crossing. The ears at the top are from four inbred strains, A, B, C and D; the second row shows F_1 ears from crosses of A by B and C by D; the bottom row shows F_2 ears from a cross of AB by CD. (From Jones.)

The proportion of homozygotes increases steadily with continued inbreeding. The closest possible form of inbreeding is self-fertilization, as seen in many plants, and the rapidity with which homozygosis is obtained in such forms is shown in Fig. 55, p. 152. Brother by sister matings, parent by offspring, etc., would plainly tend toward the same goal. For example, starting with all individuals of the population heterozygous, with continued brother-by-sister mating, Pearl has shown that the proportion of homozygotes increases in the manner indicated in the following table.

After the Indicated Numbers of Generations of Continued Brother \times Sister Mating	The Following Percentages of Homozygotes
1	50.00
2	50.00
3	62.50
4	68.75
5	75.00
6	79.69
7	83.59
8	86.72
9	89.26
etc.	

In practise, the almost universal experience of breeders seems to be that no matter how good an inbred stock may be, vigor is best maintained and improvements secured by suitable outbreeding from time to time. Probably the benefit arises out of the so-called "hybrid-vigor" to be next discussed. The application of the foregoing facts to man in the matter of marriage between close relatives is obvious (see page 222).

Heterosis.—It has long been recognized that crosses between different strains or races of plants or animals may produce offspring more vigorous in many respects than either parent type. The condition is often spoken of as "hybrid vigor" and, by the geneticist is termed *heterosis*. It is most markedly in evidence when two highly inbred strains (produced by repeated matings of near relatives) are crossed. Two pure inbred lines of corn, for example, have been known upon crossing to produce progeny with a yield that is twice as great as that of either parent strain, and to be otherwise more vigorous. In animals,

Wright found likewise that crosses between different inbred families of guinea-pigs resulted in a gain over either parental stock of twelve per cent. in weight, sixteen per cent. in size and number of litters, twenty per cent. in resistance to tuberculosis and eleven per cent. in reduced mortality. Compounding such separate gains as he could detect in F_1 hybrids produced by such crossing (*i. e.* outbreeding) he estimates a total advance of over eighty per cent. The explanation seems to be that inbreeding tends to produce a great degree of homozygosity in the traits of a stock. For many quantitative characteristics, that is, characteristics which can be expressed by more or less of a given quantity or condition, such as size, vigor, fertility, yield, rate of growth and the like, the characteristic in question is the resultant of a number of different cumulative factors. The corresponding characteristic in the other strain is likewise the expression of multiple factors, some or many of which, however, differ from those in the first strain. The result is that when the two strains are crossed a summation of different factors occurs so that in the hybrid individual there is an increased number of positive or dominant factors which enter into the upbuilding of the traits in question. The maximum effect occurs only in the first generation following the cross, however, so that if cropping, in corn, for example, is to be undertaken on this basis, the grower should grow new cross-bred seed each year instead of selecting seed from the F_1 hybrids. The reason is obvious when it is recalled that in the germ-cells of such F_1 heterozygotes segregations occur again, and the new crop, as a result of the various chance combinations, will not breed true to the F_1 parent type. The geneticist Jones secured even more extensive yields of corn than through simple heterosis by combining four inbred strains. Strain A was crossed with strain B, for example, and then strain C with strain D. The two F_1 progenies thus secured were again cross-bred and the resulting "double-crossed" progeny showed a considerable increase in yield over any of the parent types as well as over other strains of corn grown by the usual method. (Fig. 66, opposite p. 174).

CHAPTER XI

THE QUESTION OF BLENDING INHERITANCE. CONSTANCY OF GENES

We come now to certain types of inheritance in which there seems to be a true fusion or blend of the contributions from the two parents, the intermediate condition apparently persisting in subsequent generations without segregation. Numerous cases of "blending" inheritance have been cited in earlier literature of heredity, but as our knowledge of genetics has progressed many experimental breeders have come to believe that the blends in such cases are apparent rather than real and that the phenomena can be best explained on a non-blending unit-character basis, just as we would explain ordinary Mendelian phenomena.

Multiple Factors.—To get their point of view we may review certain experiments on wheat made by Nilsson-Ehle, together with their Mendelian interpretation. Nilsson-Ehle found that a certain brown-chaffed wheat when crossed with a white-chaffed strain yielded a brown-chaffed hybrid, apparently in accordance with the simple principle of Mendelian dominance. But these heterozygous brown-chaffed individuals did not in turn give the expected ratio of 3:1 in the F_2 generation but a ratio of 15 brown to 1 white, and furthermore the browns were not all of the same degree of brownness. To be exact, from fifteen different crosses of the strains he obtained 1,410 brown-chaffed and 94 white-chaffed plants.

This apparent anomaly in segregation was easily explained, however, when it was finally figured out that there were really two independent genes for brown color, either of which alone could produce a brown individual, but when combined produced individuals of correspondingly deeper shades of brown. In such a case then Nilsson-Ehle discovered that he was dealing merely with a Mendelian dihybrid where two different genes B and B' are involved. The original brown wheat had both B and B' and the original white b and b' . Thus the two formulæ were respectively, $BBB'B'$ and $bbb'b'$. The formula for the F_1 heterozygote was therefore $BbB'b'$. The four possible types of gametes

for male and female are BB' , Bb' , bB' , bb' , and the tabulation would be as follows:

	BB'	Bb'	bB'	bb'
BB'	$BBB'B'$	$BBB'b'$	$BbB'B'$	$BbB'b'$
Bb'	$BBB'b'$	$BBb'b'$	$BbB'b'$	$Bbb'b'$
bB'	$BbB'B'$	$BbB'b'$	$bbB'B'$	$bbB'b'$
bb'	$BbB'b'$	$Bbb'b'$	$bbB'b'$	$bbb'b'$

It will be observed that there are more brown determiners in some combinations than others. For instance one of the sixteen contains four such genes, viz., B , B , B' , B' , four contain three genes, six contain two, four contain only one, and one contains none. Thus all but one of the sixteen contain at least one gene and will therefore be brown in color but the depth of color will depend on the number of brown determiners in a given individual. That is, the effect is cumulative; duplication of a unit increases the intensity of the character. This is more graphically represented in Fig. 66, facing p. 174. The largest number of similar individuals, six in all, contain two genes each and represent an intermediate "blend" between the original brown-chaffed and the white-chaffed strains. The deeper and the lighter browns due to more or fewer genes in an individual would if one did not know the units in this case look like the fluctuations around this average which we might expect in a blend.

Nilsson-Ehle found another significant case in wheat where one particular red-grained strain of Swedish wheat when crossed with white-grained strains produced red-grained offspring, but when these were interbred the F_2 generation gave approximately sixty-three red to one white-grained individual. Here it was found that in the original red wheat there are three separate genes which act independently of one another in heredity, any one of which would make red color; and that they simply follow the Mendelian laws for a trihybrid.

Such Cases Easily Mistaken for True Blends.—If we should tabulate the possible combinations as we did the dihybrid we should see that we would get individuals having varying numbers of red determiners. Only one of the sixty-four possible combinations would be without a factor for red. Of the sixty-four, one would have six genes for red, six would have five, fifteen would have four, twenty would have three, fifteen would have

two, six would have one, and one would have none. Since here every additional red factor means deeper redness in the individual there would be varying degrees of redness in the F_2 generation with those having three genes the largest group, standing apparently intermediate. Not knowing the factors involved we might easily mistake such a case for a true blend with fluctuations about an average intermediate form. Nilsson-Ehle finally proved his interpretation by rearing an F_3 generation from isolated and self-fertilized plants of this F_2 generation.

This same principle of the cumulative action of *multiple factors* has been established by various other investigators. Thus both Emerson and East found it applicable to various color, size and other quantitative characters in corn; Castle, to ear-length, skeletal parts and other size relations in rabbits; Phillips, to size inheritance in ducks, and Punnett and Bailey, in fowls; Hoshino, to flowering time of garden peas; Gross, to size and shape of peppers; and Davenport, to skin-color in man. As the number of different pairs of determiners increases it can readily be seen that the number of apparent blends of different degrees of intermediacy between the two extremes would rapidly increase.

The effects of *multiple factors*, although similar and cumulative, are not always necessarily equal. Sometimes two or more pairs of genes have similar but not cumulative effects. Such factors are called *duplicate factors*. Two different sets of factors responsible for the triangular shape of the seed capsule in the shepherd's purse discovered by Shull, is a well-known example.

Most Geneticists Question the Existence of Real Blends.—The reputed "blending inheritance" of earlier investigators, particularly where the character is quantitatively expressed as more or less of a given size or amount, seems on careful experimental analysis to be resolvable into factorial inheritance which follows Mendelian rule. The observed facts are best explained at present by regarding them as due to the combined action of several independent factors.

CAN THE CONSTANCY OF GENES BE ALTERED BY SELECTION?

Still another important question concerning unit characters which requires consideration is that of whether the limits of a unit character can be extended or narrowed through selection. That is, choosing a given character, can it be made to become larger and larger in successive generations by selecting each

time for breeding purposes individuals which show it most extensively, or conversely, can it be pushed more and more toward the vanishing point by selecting those individuals in each generation which express it most feebly?

Pure Lines.—Before attempting to handle this problem



FIG. 67

Diagram showing five pure lines and a population formed by their union (from Walter after Johanssen).

understandingly it will be well to consider some of the work on so-called *pure lines*. Professor Johanssen found that in beans, for example, the seed weight of an ordinary lot of a

common variety fluctuated evenly about a mean weight. For instance, in Fig. 67, p. 180, which represents a series of glass tubes containing beans, the beans in each horizontal row are assorted according to weight, all beans of the same weight being placed in a single tube. It will be seen in the bottom row marked "population" that seventeen sizes were detectable and that they fluctuate fairly evenly around an average size, the comparatively large and comparatively small ones being few. For convenience we may speak of all those which were above the average in weight as varying in the plus direction or showing plus variation and those below the mean as varying in the minus direction or showing minus variation. Johanssen made a series of experiments to see if by breeding from plus variants only, he might not secure a strain showing increased average weight each successive generation, ultimately attaining a plus limit clear beyond the greatest weight found in the original population. He discovered, however, that he could not spring the upper or plus limit in this way. At first by selecting the very heaviest beans, he could, it is true, get a somewhat higher average weight for the total progeny but he could not transcend the upper limit. In the bean, since it is ordinarily self-fertilizing, it is easy to secure a single hereditary line, so Johanssen next made a series of studies of the isolated progeny of single beans. He found that in this way he could separate out strains which varied around a certain mean but a mean which was different in the nineteen different cases he had under investigation. These separate strains he called "pure lines" and he defined a pure line as "the descendants from a single homozygous organism exclusively propagating by self-fertilization."

Selection within Pure Lines without Effect in Beans.—

Johanssen found that selection within a pure line was wholly without effect, a small individual would produce progeny which would run the whole gamut of sizes from the smallest to the largest found in its own pure line, and likewise for a large individual. He could only conclude then that in starting out he had not had a homogeneous population but one which was in reality a mixture of several strains each with its own average of fluctuation, and that what he had succeeded in doing was to isolate various of these strains. The fluctuations around the average in a pure line were probably due merely to the varying action of external circumstances. The positions of the pods on the plant or the

beans in a pod, for instance, might influence the conditions of nutrition in such a way that some beans would grow larger than others. Such fluctuations as these were evidently not inherited. Fig. 67, p. 180, rows 1 to 5, represents five such pure lines, and the bottom row marked "population" shows the general population formed by their union. Tubes containing beans of the same weight are placed in the same vertical row. It is evident from the diagram that the commonest size in one pure line may be of rare or infrequent occurrence in another pure line, as in pure lines 2 and 3, or 3 and 4. It is clear that by selecting the very largest seed in a mixed population and by continuing this in successive generations, a certain shifting of the average toward the plus side would be accomplished at first but ultimately the pure line showing the greatest weight would be isolated and this, then, could not be further improved upon by selection. The earlier selection would accomplish merely the weeding out of lighter strains. '

Selection Usually a Sifting Out of Pure Strains.—There is increasing evidence that in much of our selection work with plants and animals in which we formerly believed we were actually increasing small continuous variations in a particular direction we were in reality merely sifting pure lines out of a mixed population, and that after this was once accomplished our further efforts were unavailing. For although according to Johannsen pure lines are "the progeny of a single self-fertilized individual" it is clear that in breeding from two separate individuals if the germinal determiners of a particular character are the same in each, their progeny, so far as this particular character is concerned, will constitute a pure line.

Professor Jennings likewise has shown in the case of *Paramecium*, a microscopic protozoan which reproduces asexually by division, that although the general population will give what is known as a *normal variability curve*, nevertheless the population is not a homogeneous group of fluctuating individuals as the plus and minus variations around a mean would indicate, but is in reality a composite of smaller distinct groups each with its own mean. In *Paramecia*, therefore, Jennings also arrived at the conclusion that selection within a pure line is without effect. Fig. 68, p. 183, is a diagram showing the relative sizes of eight different races which Jennings found in a group of *Paramecia*. Each horizontal row shows the range of fluctuation in a single

race. The average or mean size for the entire population is at the vertical line. The mean size of each race is indicated by a cross placed above the individual showing this average size.

The implication of these particular experiments is that a pure line once established, man is powerless to secure through selection any further progress in the particular character in which he is interested. He must await a favorable mutation. Johannsen, himself, however, reports that mutations do arise from time to time within his pure lines of beans. There is no evidence, however, that selection of itself had anything to do with the

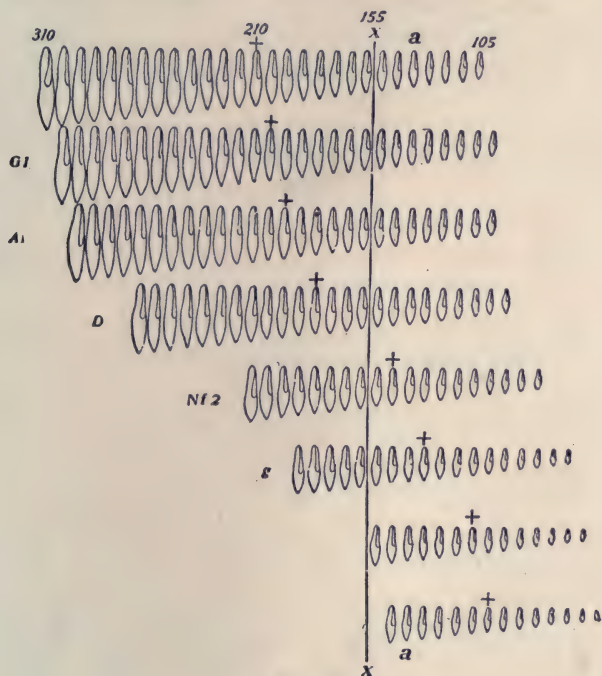


FIG. 68

Diagram showing range of fluctuations in each of eight pure races of *Paramecium*. Each horizontal row represents a single race. The cross is placed above the individual showing the mean size in each race. The mean for the entire population is at the vertical line (from Jennings).

appearance of the new mutation beyond increasing near the plus limit the total number of individuals in which the favorable mutation might occur.

The connection between this earlier work in pure lines and

our initial query as to whether the constancy of genes can be altered by selection is plain. Professor Jennings' statement that, "Until some one can show that selection is effective within pure lines it is only a statement of fact to say that all the experimental evidence we have is against it," is equally applicable to unit-characters in general.

However, in *Diffugia*, a species of protozoa which secretes a shell around itself, Professor Jennings himself found a form in which, in two strains at least, selection was effective with reference to such characters as the number of spines on the shell, the length of the spines, the number of teeth about the mouth of the shell, and various dimensions of the shell, even when the organisms were kept as nearly as possible under the same conditions. In the one strain 495, in the other 1,049, descendants were studied. Each strain originated from a single asexually reproducing parent. Such a progeny resulting from the continued division of an original individual is technically termed a *clone*.

Jennings summarizes the main facts of his experiments as follows:

"(1) Hereditary variations arose in some few cases by rather large steps, which might be called mutations, or saltations.

"(2) But the immense majority of the hereditary variations were minute gradations. Variations are as continuous as can be detected.

"(3) Hereditary variations occurred in many different ways, on many diverse characters: the number of spines; the length of the spines; the size of the body; the number of teeth. There was no single line of variation that was followed exclusively, or by the great majority of cases.

"(4) Any set of characters gave rise to variations independently of the other characters. Thus many diverse combinations of characters arose; large animals with long spines; small animals with long spines; large animals with short spines; short animals with short spines, and so on for other sorts of combinations.

"(5) The hereditary variations which arose were of just such a nature as to produce from a single strain the hereditary different strains that are found in nature."

Root and Hegner, two of Jennings' associates, working independently on protozoa allied to *Diffugia* found, furthermore, that in these forms also heritably diverse strains could be isolated by selection from a single stock reproducing by fission.

Just what the significance of the contradictory result obtained with protozoa is is not yet clear. Jennings himself apparently believes that his results from *Diffugia* are more significant than those from *Paramecia* because of the greater abundance and definiteness of the characters found in *Diffugia*. In other words, one can detect the hereditary changes which might occur in *Diffugia* more readily than in *Paramecia*. As indicative that less readily observable changes might be going on in such forms as *Paramecia*, Jennings points out that Middleton, using an infusorian (*Stylonychia*) allied to *Paramecium*, selected for slowness of fission rate and rapidity of fission rate for hundreds of generations among the offspring of an original single individual and was able to establish two distinct strains.

While he does not deny that the main visible effect of selection in a population of organisms consists merely in isolating individual strains which possess the characteristics that one is selecting, Jennings is convinced that in certain cases selection is effective in obtaining actual hereditary extensions of the conditions to be found, although he adds, "I am personally convinced that there is a difference between organisms as to the frequency with which hereditary variations occur." The main fact he emphasizes, however, is that in such forms as *Diffugia* "gradual inherited variations are occurring, so that in the course of time many hereditary diverse families arise from one. In other words, if we study these organisms with sufficient minuteness and perseverance, *we see evolution occurring.*"

When it comes to many-celled organisms, selection within a pure line has, as with Johannsen's beans, largely proved futile. Where an apparent modification of an organism has been secured in the ordinary run of plants or animals it seems not improbable that the apparent effectiveness of the selection has been secured through the accumulation or dissipation of *modifying factors* which increased or diminished the effect of the original or fundamental gene, as next described under the discussion of the hooded pattern in rats. In the many-celled animals, most nearly analogous with selection in protozoa would probably be selection within a parthenogenetic line. This has in general been ineffective, with the exception of the cases reported by Banta for certain small crustaceans known as daphnids.

Selections in Hooded Rats.—A hooded rat is one in which typically the coat of the head, shoulders and middle of the back

is black, that of the rest of the body, white. There is considerable variation in the extent of the pigmentation, however, ranging from individuals with black head and neck only, to forms with the entire back as well as head and neck, black. The hooded pattern behaves as a Mendelian recessive when crossed with the "self" (that is totally pigmented) condition of some rats, or the white-bellied (so-called Irish) condition characteristic of others. Castle and Philips sought to extend the limits of the hooded pattern by selection. During fifteen generations they selected for extreme degree of colored coat and succeeded in securing animals with a considerably greater extent of pigmentation (Fig. 69, below) than any of the original stock with which they started.

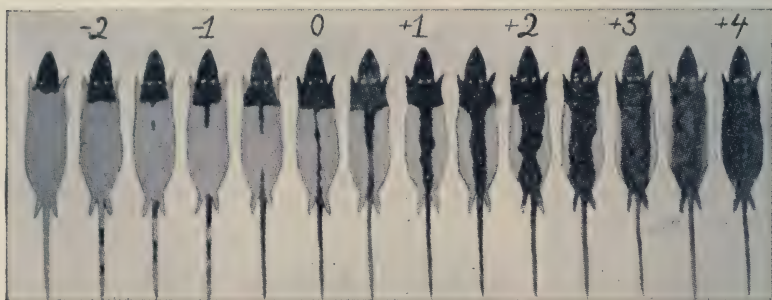


FIG. 69

Series of grades of plus and minus variations of the white spotting pattern of hooded rats, obtained through selection in successive generations (after Castle).

Conversely by selecting generation after generation the less pigmented individuals they gradually secured a decided diminution in the pattern, finally obtaining "an animal having less pigment than any known type other than the albino."

In this experiment it would seem, at first sight, that the rats in question possess a factor or factors for hoodedness which were undergoing fluctuations and that selection was inducing inheritable changes in both a plus and a minus direction. However this is probably not the true explanation. Certain test experiments showed rather that typical hoodedness is due to the presence of a fundamental gene for hooded pattern cooperating with a number of modifying factors and that what had really been accomplished was the sorting out of different com-

binations of these from heterozygous ancestors. As seen in the discussion of blending inheritance, in the progeny of heterozygotes where more than one determiner is involved as the basis of a character, certain individuals will receive a number of these in excess of that carried by the parents while others receive fewer. The result as a whole is more or less variability among the progeny. An effective plus or minus selection within certain limits, depending on the number of factors concerned, would be possible without necessitating the fluctuation or progressive variation of any individual Mendelizing unit.

That the changes in question were the result of changes in the total complex of factors instead of in the individual genes for the hooded pattern, Castle showed by recovering the typical hooded pattern again through repeatedly crossing individuals of his selected plus and minus extremes respectively with a wild non-hooded race which presumably reintroduced the original modifying genes.

Constancy of the Gene.—At present in spite of the somewhat conflicting evidence, it is the belief of most geneticists that the underlying genes of so-called unit-characters are not varied by selection. Presumably we can vary only the combinations into which such genes enter. Character changes produced by selection in higher animals at least, are apparently not quantitative or qualitative changes in individual genes, but are due to the supplementary or modifying action of other genes. Experiments so far attest in general the remarkable constancy of the gene. The question can not be regarded as closed, however, and further experimentation is greatly needed. The sporadic changes known as mutations which occur in genes from time to time are to biologists still an unsolved mystery.

CHAPTER XII

LINKAGE, CROSSING OVER, AND THE LINEAR ARRANGEMENT OF GENES

Parallel between the Behavior of Mendelian Factors and Chromosomes.—The question arises as to whether there is any evidence from the study of germ-cells themselves to bear out the Mendelian conception of separation of contrasted characters in the gametes of the F_1 generation. In the discussion of the maturation of germ-cells (Chap. VI) it has already been seen that the chromosomes of the germ-cells are in all probability arranged in homologous pairs, one member being of maternal and the other of paternal origin, and that furthermore they are closely associated with the phenomena of heredity. And since in maturation there is an actual segregation of the chromosomes into two sets, half going to one cell and half to its mate, a physical basis adequate to the necessities of the case is really at hand. It will be recalled that the individuals of a pair separate in such a way at the reduction division that the paternal member goes to one cell and the maternal member to the other, although each pair seemingly acts independently of the others with the result that any mature germ-cell may contain chromosomes from each of the original parents but normally never the two chromosomes which earlier made up a pair. The close parallel between the behavior of chromosomes and the behavior of Mendelian factors, although the two sets of phenomena were discovered wholly independently of each other, is obvious. If we suppose that each chromosome bears the gene of a Mendelian character and that chromosomes bearing allelomorphic genes make up the various pairs which are seen in the early germ-cells of an individual before reduction occurs, then the segregation of the individuals of an allelomorphic pair into different gametes must result in consequence of the passing of the corresponding chromosomes into separate gametes. Fig. 70, p. 189, from Professor Wilson, represents equally well the segregations of pairs of chromosomes or pairs of Mendelian characters.

Linkage.—Since there are far more pairs of allelomorphic characters in an individual than there are pairs of chromosomes, it is obvious, if the chromosomes are the actual carriers of the genes, that each chromosome bears more than one gene. As a matter of fact, modern geneticists are finding whole blocks of hereditary characters which enter together into the construction of the new individual and which segregate out in the next generation in the same associated form, as if their genes all rode

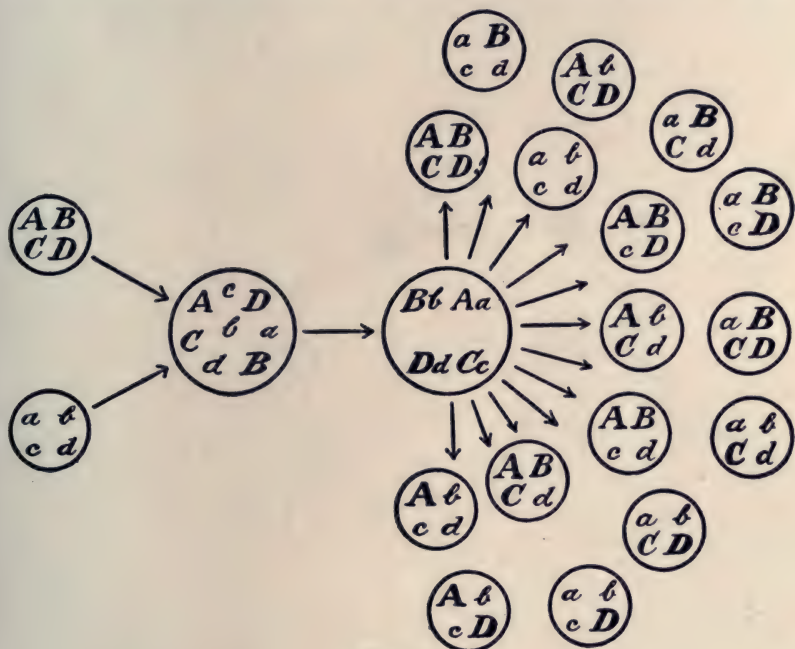


FIG. 70

Diagram showing union of factors from the two separate parents in fertilization and their segregation in the formation of germ-cells (after Wilson). With four pairs of factors (Aa , Bb , Cc , Dd), sixteen types of gametes are possible, as shown in the series of small circles at the right. The same diagram equally well represents the pairings and segregations of chromosomes.

in the same vehicle; and the evidence indicates that the conveyance for each such group of genes is a single chromosome. In no kind of plant or animal have more groups of linked characters been found than there are pairs of chromosomes. Since in all probability one member of each chromosome pair is of

maternal and the other of paternal origin, and inasmuch as they separated in the reduction division, one going to one germ-cell, the other to another, it is easy to see, provided their genes are located in the chromosomes, how such linked groups of characters are shunted to and fro. This tendency of certain genes to stay together in hereditary transmission Morgan has termed *linkage*.

The "free assortment" of pairs of characters as described by Mendel, therefore, is apparently an actuality only in so far as the genes of the different pairs of characters being considered are located in different pairs of chromosomes. Whatever assort-

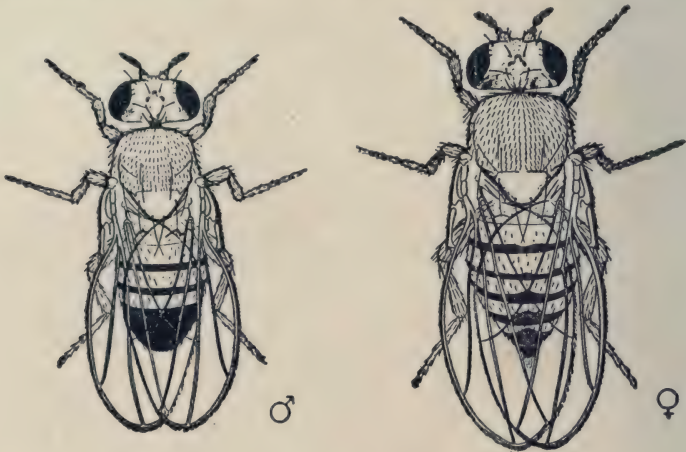


FIG. 71

Male and female fruit fly, *Drosophila melanogaster* (after Morgan).

ment there is based on the behavior of the chromosomes during the reduction division and the ensuing fertilization. As long as a given chromosome retains its identity the genes which are a part of it will remain together. Mendel, luckily, in his experiments, hit upon pairs of characters the genes of which were not resident in the same chromosome pair, and thereby discovered his principle of free assortment.

In the hands of Professor Morgan and his associates, the fruit fly, *Drosophila*, has been of inestimable service in determining the real physical basis of inheritance. For not only has it numerous well-defined characters and the capacity of pro-

ducing two or three hundred descendants every ten or eleven days, but it has very few chromosomes and certain of them quite unlike the others in size and appearance. In the species known as *Drosophila melanogaster* (Fig. 71, p. 190), there are only four pairs of chromosomes in the body-cells and early germ-cells (Fig. 72, below), and this means four single chromosomes in each mature germ-cell. Three chromosomes of such a single set are large and one is very small. Furthermore one of the three larger ones is a sex-chromosome to which can be assigned characters which show sex linkage. In these flies over four hundred different characters have been identified of which some two hundred have been tested genetically in literally millions of individuals and found to fall into four linkage groups corresponding to the four pairs of chromosomes. Three of these groups contain many characters each. In one, over one hundred have been identified. One of the sets is sex-linked and may therefore be assigned to the sex-chromosome. The other two large groups of genes are probably associated with the two remaining large chromosomes, while a small group in which only three characters have been discovered so far is probably referable to the smallest chromosome.



FIG. 72

Diagram of female and of male group (duplex) of chromosomes of *Drosophila melanogaster* showing the four pairs of chromosomes. The hook on the Y chromosome is characteristic. The members of each pair are usually found together, as here (after Morgan).

Linkage has been observed in various other organisms besides *Drosophila*. It was first discovered, in fact, by Bateson and Punnett in sweet peas. They found that flower-color and pollen-shape tended to stay together in inheritance when a race with purple flower and long pollen grains was crossed with one having red flowers and round pollen grains. They spoke of the condition as the "coupling of factors."

The following representative types of plants and animals in which linkage has been found shows that the phenomenon is probably a universal one (in each case the authority is named in parenthesis): Sweet pea (Bateson and Punnett); garden pea (White); corn (Emerson, Jones, Lindstrom, Breggar); wheat, snapdragon (Bauer); evening primrose (Shull); *Primula*

(Altenberg, Gregory); tomato (Jones, Lindstrom); oats, beans (Surface); silkworms (Tanaka); grouse locust (Nabours); *Drosophila virilis*, *D. repleta* and *D. busckii* (Metz); pigeon (Cole and Kelly); rabbit (Castle); mouse (Castle and Dunn); rat (Castle and Dunn, Olsen).

Crossing over.—In such linked groups of characters, however, exchanges sometimes occur as if the residents of one set exchanged places with the corresponding residents of the other set. Technically this is termed “crossing over.” It can be explained on the supposition, based also on a certain amount of visible evidence in the chromosomes themselves, that the paired chromosomes lying side by side occasionally get twisted around each other so that when they finally separate in the reduction

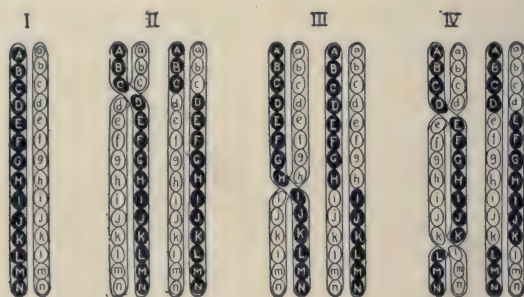


FIG. 73

Diagram illustrating the probable mechanism of crossing over.

division, corresponding pieces of the original pair, relating genetically to the same features of the body, have exchanged places. This chromosomal explanation of the crossing over discovered by geneticists is known as the *Chiasmatype theory*. How possibly this is effected is shown in Fig. 73, above, where the different qualitative regions of the chromosomes are indicated by letters. In Fig. 73, I represents the usual occurrence; each chromosome remains intact upon separating after synapsis. In II, a crossover is represented as occurring between C and D, with the result that the two ends of the chromosome become exchanged. In III, the crossover is at a different point. Fig. 73, IV, represents a double crossover, for the occurrence of which there is good genetical evidence.

In actual breeding experiments, under uniform environmental

conditions the various characters of a linkage group show different though constant crossover values, hence the inference is that their genes are linearly arranged in the chromosomes and that they maintain the same relative positions. Obviously crossing over is likely to occur oftener between factors which are far apart in the chromosome than between those which are near together. Referring to Fig. 73, for example, a crossover at any point between the ends of the chromosomes would put A in one chromosome and N in the other, but a crossover at only one particular point could separate A from B, F from G, or L from N; or in other words, the nearer two genes are together the less likely they are to be separated by such cross exchanges. Utilizing this inference in their analysis of the genetical behavior of *Drosophila*, Professor Morgan and his collaborators are making the bold attempt to map the chromosomes themselves and tell us where, relatively, the genes of certain characters are located in each respective chromosome. The correctness of their inference is attested by the fact that, for short linkage distance at least, they can predict in advance of the actual mating how great a proportion of crossing over there will be between certain characters.

As an illustration of crossing over some of the well established cases in *Drosophila* may be cited. The ordinary wild type of this fly, for example, has *gray body* and *long wings*. When it is crossed with a type which sometimes occurs having *black body* and *vestigial wings*, the F_1 hybrids have *gray bodies* and *long wings*. In other words gray body and normal wing are dominant. When, in order to reveal what is present in a recessive condition in such a heterozygote, the usual test of crossing the hybrid back to the recessive parent type is made, a different result is obtained when the male is the heterozygote from that secured when the female is the heterozygote. When the male is the hybrid fly and the female is the recessive black vestigial type, only two classes of offspring appear; namely, the gray-long of the one grandparental type and the black vestigial of the other. Evidently the two characteristics of gray body and long wings which originally entered the cross together stay linked and act as an individual unit in the F_1 heterozygote as do also black body and vestigial wings. In other words linkage is complete for the characters in question in the germ-cells of the hybrid male fruit fly. If, however, the hybrid female fly is back-crossed

with the black-vestigial male, then four types are produced—the same four types that are expected when independent assortment of genes occurs as in typical Mendelian segregation, but in a wholly different proportion. Instead of the 25 per cent. each of gray-long, black-vestigial, gray-vestigial and black-long which would be expected from free assortment, Morgan obtained 41.5 per cent. each of gray-long and black-vestigial and 8.5 per cent. each of the new phenotypes black-long and gray-vestigial. The new types represent crossovers, or in terms of the chromosome theory, breaks in the union of the linked genes in question within the chromosomes. That is for these particular characters 17 per cent. ($8.5 + 8.5$) of the individuals of the new generation were of the crossover type and 83 per cent. of the original or non-cross type, or in other words crossing over occurs in about 17 per cent. of the gametes of the F_1 female. There is said, therefore, to be 17 per cent. of crossover. Linkage varies with different genes. For example, *yellow-body* and *white-eye* give 1.2 per cent. of crossover in *Drosophila*, *white-eye* and *bifid-wing* 3.5 per cent., while two characters called “star” and “speck” give 48 per cent. of crossovers.

As stated, crossing over seems not to occur in the male in *Drosophila*. In the silkworm, on the other hand, it occurs in the male but apparently not in the female. Why this is true is unknown. In other plants and animals, so far as known, crossing over occurs in each sex. Outside of *Drosophila* our information about crossing over, however, is very meager.

Chromosome Maps.—If the assumption is valid that the frequency of crossing over between two characters represents the relative distance of their genes apart in the chromosome—which carries with it the inference that their location in the chromosome is always the same—then it should be possible to determine the relative locations of the known genes in a chromosome and thus actually map the chromosome. To secure a scale of measurement Morgan takes one per cent. of crossovers to represent one unit of distance between the two genes in question. In the case of black-body and vestigial-wing, therefore, since there was 17 per cent. of crossovers the genes for these two characters are 17 units apart. As we have seen, *yellow-body* and *white-eye* gave a crossover value of 1.2 units, and *white-eye* and *bifid-wing*, a crossover value of 3.5 units. The question next arises of what the linear order of the three genes in ques-

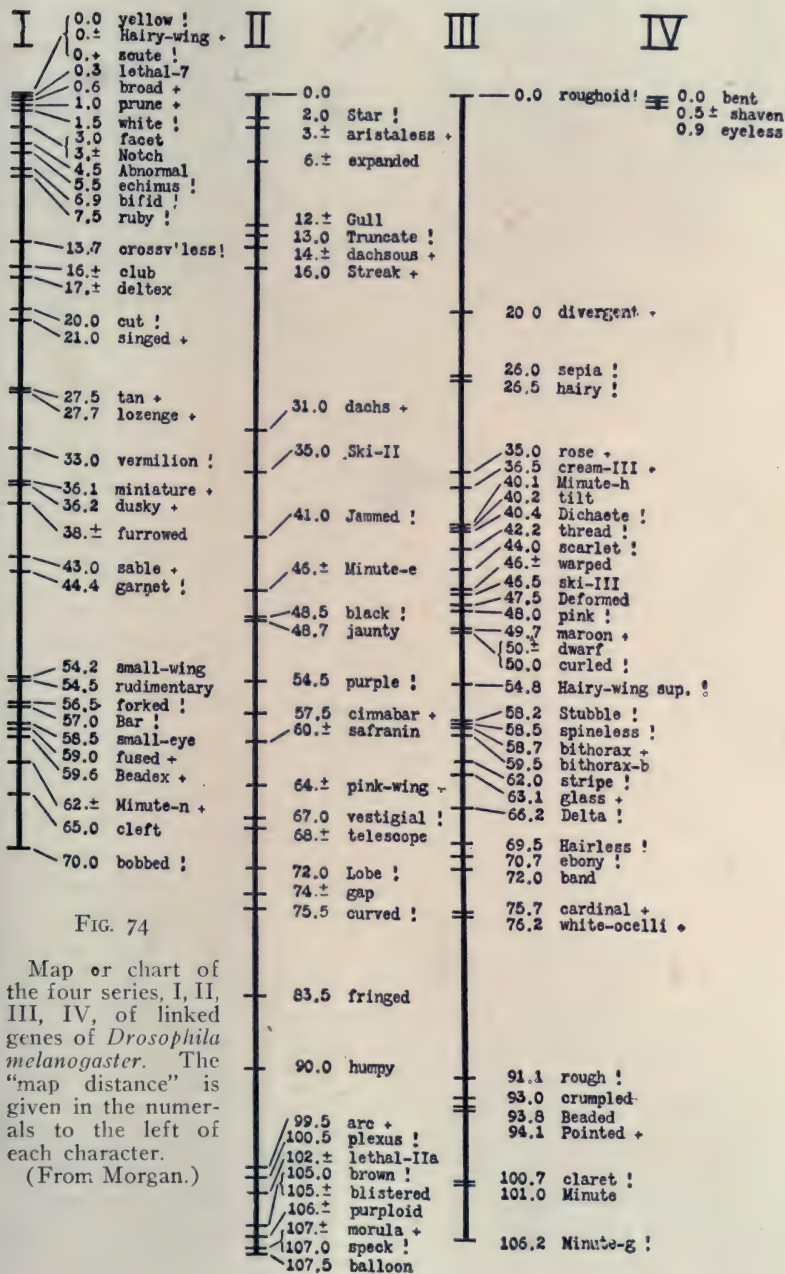


FIG. 74

Map or chart of the four series, I, II, III, IV, of linked genes of *Drosophila melanogaster*. The "map distance" is given in the numerals to the left of each character.

(From Morgan.)

tion—yellow-body, white-eye, bifid-wings—is in the chromosome. Is it, for example, yellow-bifid-white, or yellow-white-bifid? The obvious way of determining this, of course, is to find by breeding tests the crossover values of yellow-body and bifid-wings. Since the genes for yellow-body and white-eye are 1.2 units apart and those for white-eye and bifid-wing are 3.5 units apart, then if the gene for bifid-wing lies between them the crossover value of yellow-body and bifid-wings should be 2.3 (i. e., $3.5 - 1.2$) but if beyond white, then it should be 4.7 (i. e., $3.5 + 1.2$). Breeding tests showed it to be the latter, namely, 4.7 units. The linear order of the three genes is therefore yellow-white-bifid. By thus finding its linkage value with other units of known position it is evident that the relative location in the series of any new or uncharted gene may be determined. Sturtevant first made such a map for the genes in the X-chromosome of *Drosophila*. The relative positions of more than 150 unit factors have now been determined in the four chromosomes of *Drosophila melanogaster*. This is one of the most notable achievements of twentieth century biology. Fig. 74, p. 195, represents maps of these chromosomes showing the relative positions of some of the genes which have been located. The numerals refer to distances from the end of the chromosome, as determined by percentages of crossing over (corrected for double crossing over).

Double Crossing Over.—In the case of certain widely separated genes experimental results were obtained which were at variance with the theoretical expectation based on the hypothesis of simple crossing over. Thus when *white-eyed* flies were crossed with *bar-eyed* flies the percentage of crossover was 44. Calculations, however, made by adding together the shorter distance which had been determined for certain genes between “white” and “bar” gave a sum of 55. That is the actual percentage of crossover fell short of the expected percentage. Similar shortages in other long distances were encountered. The difficulty was finally cleared upon the assumption that in such long distances a double crossing over occurs (see Fig. 73, IV, p. 192) in a certain percentage of cases and that thus the widely-separated genes are still retained in the original association. Since short distances are not affected by crossovers, to determine the true distance between widely-separated genes, therefore, it is more accurate to add together the sums of the

shorter intervening distances than to depend upon the results obtained by directly determining the crossover values of the distant genes themselves.

Interference.—Muller pointed out that a crossover in a particular region should, because of the physical condition involved make it improbable that a second crossover would occur very near the first. Subsequent breeding experiments confirmed his prediction. This prevention or hindrance of crossing over of the other genes adjacent to a crossover is termed *interference*.

Resumé.—From the foregoing discussion in which it is inferred that the chromosomes are the seat of the genes, the following facts are paramount:

1. The number of linkage groups is never greater than the number of pairs of chromosomes.
2. Crossing over takes place only between synaptic mates.
3. Synaptic mates, where crossing over occurs, must lie side by side with corresponding allelomorphic units opposite one another.
4. The genes of a chromosome must be arranged in a linear series and the distance between any two genes is proportional to the percentage of crossovers between them (after corrections for *double crossing*, or for *interference* are made, when necessary).

Irregularities.—Occasionally one or more chromosome pairs fail to separate in the maturation division with the result that both members of the pair pass to one pole. In this way an abnormal number of any or all of the chromosomes may occur in egg or sperm. After the fertilization in which such a germ-cell takes part there is of course an abnormal number of chromosomes in the zygote. This phenomenon was discovered by Bridges in 1913 and named by him *non-disjunction*. In attempting to explain certain unexpected ratios he obtained in his breeding experiment with white-eyed fruit flies he concluded that his results could be accounted for only upon the supposition that the two X-chromosomes had remained attached to each other and passed to one pole of the spindle during the reduction division, leaving the opposite pole without an X-chromosome. As a result, half of the mature eggs would possess two X-chromosomes and half would have none. Microscopic examination proved this to be so. Breeding tests combined with microscopic examination of the progeny showed conclusively that the sex-

linked traits he was observing always had the same distribution as that of the sex-chromosomes. Non-disjunction has since been observed not only in other chromosomes of *Drosophila* but in other kinds of organisms both plant and animal. Cases are known indeed in which the entire haploid set of chromosomes is trebled (triploidy) or quadrupled (tetraploidy) or even further multiplied, to say nothing of more irregular distributions which are known. In various primroses (*Oenothera* for example), variant forms are known which have 15, 16, 20, 22, 24, 27, 28, 29 and 30 chromosomes instead of the typical 14 of *Oenothera lamarckiana* from which presumably they sprang. Tetraploidy has been found to exist in a number of giant varieties of plants such as the primrose (Gates and others), the jimson weed (Blakeslee and Belling), the tomato (Winkler), and yet others. That not only quantitative but qualitative differences probably also arise through irregular distributions of the ordinary chromosomes (autosomes) is indicated by the well-established fact that abnormal distribution of all sex-linked characters parallels abnormal distribution of the sex-chromosomes. Thus both the regular and the irregular behavior of the chromosomes attest the importance of chromosomes as the essential mechanism of heredity.

CHAPTER XIII

HUMAN HEREDITY

I. MENDELIAN INHERITANCE

The Mendelian Principles Probably Applicable to Many Characters of Man.—We are really just beginning to make the proper observations and collect the necessary data with reference to the application of Mendelian principles to the traits of man. Yet brief as has been our study we have disclosed much significant evidence which makes it seem highly probable that many of his characters, good and bad, of mind and body are as subservient to these laws as are the traits and features of lower forms.

Difficult to Get Correct Data.—While it must be said that in many cases no simple form of Mendelian tabulation has been unequivocally established, yet the general behavior of the various inheritable traits in question is so obviously related to the conventional Mendelian course that there seems little reason for doubting that they are at bottom the same. Failure to obtain exact proportions may be attributable in part to the probability that what we loosely regard as a character should in reality be analyzed into more elemental components, and above all to the fact that from the very nature of the conditions under which human records must be obtained, there is considerable chance of inaccuracy or error in such accounts. How many human traits follow Mendelian rules remains largely for future investigators to establish.

We are handicapped at the outset in man by the many difficulties of getting correct data from the genealogies on which we must depend, or in fact of getting any genealogy at all, for in this country at least, most families keep imperfect records of births and deaths and most of the institutions for the various kinds of defectives have little in their records that will help us in following out hereditary conditions. Then in matters of disease we meet with the fact that many former diagnoses were erroneous. In yet other cases, and this is particularly true among mental

and moral defectives, we are often not sure of the paternity of a given child. Furthermore, one is likely to be misled by the proportions which may occur in the very limited number of children of any given couple.

Still other difficulties exist. Among these is the fact, for example, that in many cases of defect or susceptibility to disease, a given individual in the stock may have the trait in an expressible and transmissible form, yet it never comes to expression because that individual has been fortunate enough to escape the environmental stimulus which would call it forth. Thus one highly susceptible to tuberculosis might escape infection, or persons hovering on the verge of insanity might never receive the precipitating stimulus which would topple them into actual insanity; yet each would be wrongfully recorded in a genealogy looking to such traits as perfectly normal. Or again if it be a question of intellectual brilliancy as shown by accomplishment in the realm of scholarship, or of worldly affairs, the ones who although possessing them have had no chance to display unusual talents would be tabulated as average whereas in fact they should be recorded as of high rank. That this is particularly likely to happen in the case of women is evident.

A Generalized Formula for Man.—In man as in lower forms some characters or traits are due presumably to the presence of determiners or to their absence or inaction. Likewise, dominance and recessiveness are as much in evidence, for in tracing back pedigrees of various traits we find the same forms of tabulation hold good that obtain for these conditions in plants and lower animals. For typical cases in man we may use a generalized formula in which A indicates the determiner of the character (double in the individual, single in the germ) and a, its absence. Thus AA represents a condition in which similar genes have been derived from both parents and the individual is *duplex* as regards the character in question; each mature germ-cell will have the gene. Aa represents a condition in which the individual has received the gene from only one parent and is therefore *simplex* with regard to the character; half of the gametes of such an individual will have the gene and half will lack it. Lastly, aa represents absence of the positive factor. Such an individual is *nulliplex*. He or she will not have the gene represented in any of the gametes, and can not, of course, transmit a trait represented by it.

It is evident that six kinds of gametic matings are possible among individuals representing these various formulæ. These matings are as follows:

Matings	Possible couplings of gametes	Product
1. Nulliplex x Nulliplex ($aa \times aa$)	$= a \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} a =$	all nulliplex.
2. Nulliplex x Simplex ($aa \times Aa$)	$= a \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} A =$	50 per cent. with character nulliplex and 50 per cent. with it simplex.
3. Nulliplex x Duplex ($aa \times AA$)	$= a \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} A =$	all with characters simplex.
4. Simplex x Simplex ($Aa \times Aa$)	$= A \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} A =$	25 per cent. with characters duplex, 50 per cent. with it simplex and 25 per cent. with it nulliplex.
5. Simplex x Duplex ($Aa \times AA$)	$= A \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} A =$	50 per cent. with character duplex and 50 per cent. with it simplex.
6. Duplex x Duplex ($AA \times AA$)	$= A \begin{array}{c} \diagup \diagdown \\ \diagdown \diagup \end{array} A =$	all duplex.

Indications of Incomplete Dominance and of Multiple and Modifying Factors.—While in cases of strict Mendelian dominance it is not possible to distinguish directly the simplex from the duplex condition, as a matter of fact the individual of simplex constitution sometimes has the character represented in the single dominant gene less perfectly developed than in the corresponding character of duplex origin. In studying defects in man where theoretically normality is dominant, one finds it recorded with increasing frequency that such individuals are more or less "intermediate" or are "tainted" with the defect; thus showing that the defect though obscured is not wholly in abeyance. Thus individuals carrying epilepsy or feeble-mindedness which are regarded as recessive traits, while not showing specific feeble-mindedness or epilepsy, may nevertheless apparently show a neuropathic taint in the form of migraine, alcoholism or other lapse from normality. The condition is seemingly more akin in some cases to that found in the offspring of certain red flowers cross-bred with white flowers, which though

red do not show the same intensity of color as the original red parent. Just as here the single gene or single "dose" of redness is insufficient to produce the intensity of color that appears when the offspring receive two genes for red, one from each parent, so in man a single gene for normality of a specific character is inadequate in some cases to make the individual wholly normal. Other cases are probably more of the type of those in which the character in question, for instance the red color of some wheats and corn, may be produced by any one of two or three genes (multiple factors), the intensity of the characters (red color, e. g.) depending on whether one, two, three or more genes are present. In still other cases modifying factors which affect the extent to which the character develops doubtless enter.

Why after the First Generation Only Half the Children May Show the Dominant Character.—If the trait is a simple dominant one it is clear that it will appear in each generation and spring only from an affected individual. By referring back to our tabulation of possible matings on page 201 where the dominant character is represented by the letter A, this can be seen at a glance. If the trait is present in the duplex condition in one parent and absent from the other, then formula 3 applies; all children will show the trait, but in the simplex form (Aa). If the trait is present in the simplex form in one parent and absent in the other, formula 2 applies. Fifty per cent. of the children will have the character in the simplex form (Aa) which means also an even chance of transmitting it to their offspring; fifty per cent. will not inherit it and will be incapable, furthermore, of transmitting it, since they have become nulliplex (aa). In human genealogies if an individual having an unusual trait which is inherited as a dominant marries a normal person and half of the offspring show the trait this means that the parent manifesting the trait had it represented only in the simplex condition, otherwise all of the children would have shown it. If the trait is a defect all the children showing it, even though marrying normal (nulliplex) individuals, will pass it on again to half their children, but those who do not show it may ordinarily marry with impunity since its non-expression in their make-up means, as far as we know at present, that the germ-plasm has been purged of the defect and that they are therefore nulliplex with reference to it.

Eye-Color in Man.—Of normal characters in man which

follow the Mendelian formula perhaps eye-color is the best established. Brown or black eye-color is due to a *melanin* pigment absent from the blue or gray eye. That is, a brown eye is practically a blue eye plus an additional layer of pigment on the outer surface of the iris. The different shades of brown are due to the relative abundance of this pigment. Gray color and the shades of blue seem to be a modification of an original dark blue, due to structural differences in the fibrous tissues of the iris.

In inheritance brown or black is dominant to blue or gray. Hence two brown-eyed parents, if the pigment factor (P) is duplex in both (or duplex in one and simplex in the other) can have only brown-eyed children. Thus,

1. $PP \times PP = PP$, or all duplex brown.
2. $PP \times Pp = PP$ and Pp , half duplex brown and half simplex brown.

If each parent has brown eyes but in simplex condition, then one-fourth of children will have blue or gray eyes, for example,

Mating	Gametic Couplings	Product
$Pp \times Pp$	$ \begin{array}{c} P \\ \diagdown \quad \diagup \\ P \quad P \\ \diagup \quad \diagdown \\ p \quad p \end{array} $	PP , Pp , pP , and pp , or one-fourth duplex brown, one-half simplex brown, and one-fourth blue or gray.

If the parents have blue or gray eyes they do not have children with black or brown eyes, since the recessive condition in each parent means absence of brown pigment.

If the eyes of one parent are duplex brown and those of the other are blue, then all children will have brown eyes but of simplex type.

If one parent has simplex brown eyes (type Pp) and one blue (pp) then one-half of the children will have brown eyes of simplex type and one-half will have blue eyes.

Occasional objections have been raised against the Mendelian interpretation of inheritance in eye-color, but the cases cited in evidence against the theory usually narrow down to those in which the color is so diluted as to render classification uncertain. For example, hazel eyes are sometimes called gray; they belong, however, to the melanic pigmented type although the brown pigment may be much diluted and occur mainly around the pupil. Very exceptionally, apparently a genetically brown-eyed heterozygote does not develop brown eye-color, but yet retains the

capacity for transmitting it to descendants. So-called green eyes are due to yellow pigment on a blue background. In the rare cases where in the same individual one eye is brown and the other blue, the individual should probably be rated as brown-eyed on the supposition that in the one eye the development of brown pigment has in some way been suppressed. It is possible, however, that a "spot" or "pattern" factor may enter in some cases.

In certain recent studies by Winge and others, facts are coming to light which indicate that in addition to the simple pair of Mendelian factors for eye-color, a dominant sex-linked factor for brown eyes may also enter. Thus, extensive statistics collected by Hansen on 300,000 school children, as well as data obtained by others, show that there are more brown-eyed women than brown-eyed men. Also, Winge's evidence indicates that fathers heterozygous for brown eyes married to blue-eyed mothers have equal numbers of brown-eyed and blue-eyed sons, but an excess of brown-eyed daughters. Since sons do not receive the X-chromosome from their father but daughters do, if there is a dominant sex-linked factor for brownness as well as a simple dominant Mendelian factor, such an excess of brown-eyed daughters would be expected. In other words, daughters would be brown-eyed not only because of the dominant factor borne by an ordinary chromosome, but also some who would otherwise be blue-eyed, would be brown-eyed because of the factor linked with the X-chromosome. When the mother is heterozygous for brown eyes and the father is blue-eyed, however, there is an excess of both blue-eyed sons and blue-eyed daughters. This is difficult to explain unless one makes some such assumption, as does Gates, that female gametes which simultaneously contain the sex-linked factor for brown and the ordinary gene for blue, for some reason can not exist.

Hair-Color.—The inheritance of hair-color has also been the subject of considerable study and while the conditions are not so simple as in the case of eye-color, there is little doubt that it belongs in the Mendelian category. In human hair, color has as its foundation apparently two pigments, black and red. Absence of one or both or various combinations or dilutions of these seemingly account for the prevailing color in human hair. In general, dark hair is dominant to light, although because of the delay sometimes in the darkening of the hair in children

this fact is often obscured. Black is dominant to red. People with glossy black hair, according to Davenport, are probably simplex for black, the glossiness being due usually to recessive red. The expectation would be for some of the children of such a pair to have red hair.

In man occasionally a congenital white lock contrasting strikingly with the remaining normally pigmented hair occurs. It behaves as a simple dominant in heredity.

Hair-Shape.—Again, straight and curly hair seem to be distinct inheritable characters. Curly is incompletely dominant to straight, the simplex condition yielding wavy hair.

Not to enter into details of the matings, statistics gathered by Mr. and Mrs. Davenport show that, two flaxen-haired parents have flaxen-haired children; two golden-haired parents have only golden-haired children; two parents with light brown hair have children with hair of that color or lighter, but never darker; two parents each with dark brown or black hair may have children with all the varieties of hair-color. Summing together a series of recessives Davenport points out that two blue-eyed, flaxen or golden and straight-haired parents will only have children like themselves.

Irregularities.—If a dominant trait or defect depends on more than a single factor, as is sometimes the case, or if it is modified by sex or other conditions, as is true of certain characters, then we shall find some apparently non-affected individuals having affected offspring. Certain diseases, for example, are generally transmitted by affected members of the family to their children in the expected Mendelian ratio for a dominant, yet an occasional skip of a generation may appear in which an apparently perfectly normal individual transmits to his children what, except for the omission in his own case, appears to be an ordinary dominant character. This occasional lapse in the appearance of a character when theoretically it should appear is doubtless due in some instances to the fact that what is really inherited is a *tendency*, and although this is present in the apparently normal individual, for some reason the condition itself has not appeared. This might especially be true in the case of a disease which does not manifest itself until late in life. In other cases there are undoubtedly complicating accessory conditions which modify the behavior of the trait somewhat.

OTHER CASES OF DOMINANCE IN MAN

Among other normal characters in man, as far as available evidence goes, dark skin is dominant to light skin; normally pigmented condition to albino; and nervous temperament to phlegmatic.

Digital Malformations.—An interesting and easily followed defect is a condition known as *brachydactylism*, in which the digits are shortened because of the absence or rudimentary condition of one segment. The fingers, therefore, appear to be only two-jointed like the thumb. Several families showing this defect have been charted and it appears to behave as a typical dominant. In looking over such a chart (Fig. 75, below) one



FIG. 75

Diagram showing descent of brachydactyly through five generations; black symbols indicate affected individuals; ♂, male; ♀, female (after Farabee).

is struck by the fact that only half of the children from most of the matings show the defect, but when we recall that the affected parent, after the first generation, probably carried the condition in only the simplex form and married a normal individual, such a result is just what would be expected (see formula 2).

Polydactylism (Fig. 76, opposite, and Fig. 77, p. 207) is a condition in which there are extra digits on hands or feet. The character, with apparently slight exceptions in a few records, behaves as a typical dominant. Among other digital defects which are inherited as a dominant is a condition known as *syndactylism*



FIG. 76. Radiograph (Courtesy of Dr. W. B. Helm) showing polydactyly in a child's hand. For genealogy of this see Fig. 77, p. 207.

(Fig. 78, facing p. 208), in which two or more digits are fused side by side. For an example of syndactyly which seems to be in the class of sex-linked characters, see Fig. 44, p. 121.

Eye Defects.—*Congenital cataract* is another not uncommon defect in man which is usually transmitted as a dominant (Fig. 79, p. 208) with occasional irregularities. It is a condition of opacity of the lens of the eye which produces partial or total blindness. In a paper on *Hereditary Blindness and Its Prevention*, Clarence Loeb (1909) mentions 304 families of which pedigrees have been published. Of the 1,012 children in these

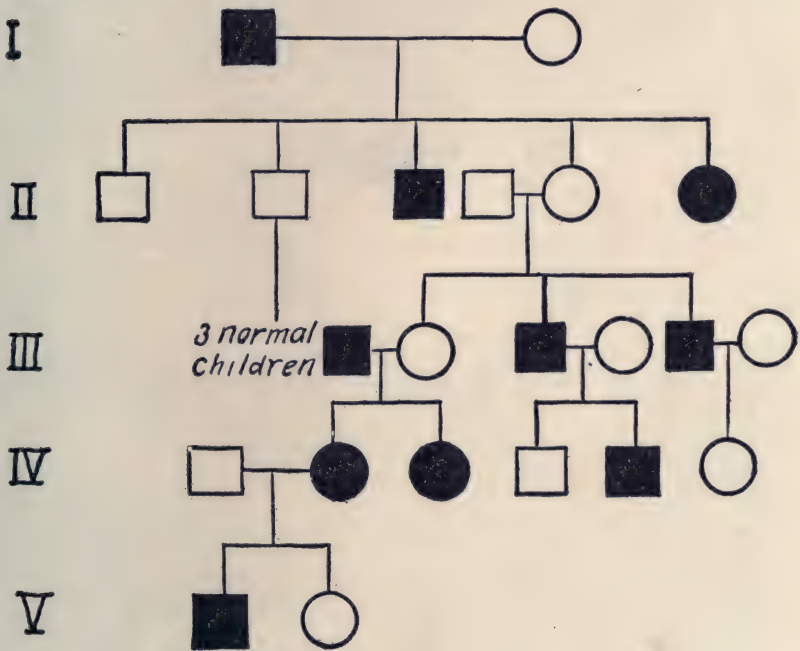


FIG. 77

Chart showing a history of polydactyly through five generations in the B—— family. The individual whose hand is pictured in Fig 76, facing p. 206, is of the fifth generation. Squares represent males, circles females.

families 589, or 58 per cent., were affected. It is obvious that this is near the expected percentage in the case of a dominant trait where matings of affected with normal individuals prevailed. An unfortunate circumstance about this malady from

the eugenic standpoint is the fact that it is frequently of the presenile form which comes on late in life so that it is usually impossible to predict whether an individual of marriageable age is immune or will later become affected.

Jones and Mason, after a review of Harman's data on congenital cataract in the *Treasury of Human Inheritance*, deny that it is inherited as a dominant. They maintain that the facts at hand better substantiate the view that it behaves as a simple recessive. This interpretation is borne out, perhaps, by a case of congenital cataract in cattle reported by Detlefsen and Yapp, which behaved as a Mendelian recessive. It is not improbable, however, that congenital cataract may be due to different factors

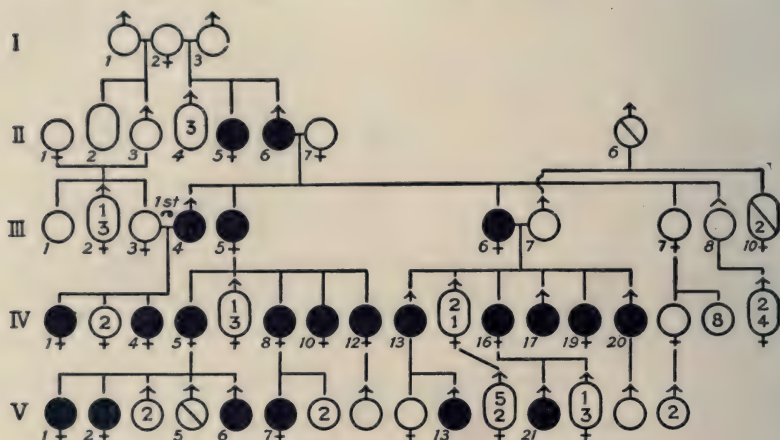


FIG. 79

Pedigree of a family with presenile cataract (black symbols); numbers in circles indicate unaffected individuals (after Davenport).

which may exhibit unlike hereditary behavior in different cases.

Another defect of the eye following the course of a dominant in heredity is a pigmentary degeneration of the retina known as *retinitis pigmentosa*. Atrophy of the optic nerve is also involved and the final result is blindness. Still another example frequently cited is that of hereditary night blindness (*hemeralopia*), a disease in which the affected person can not see by any but the brightest light. In most affected families the final outcome is usually total blindness. One of the most remarkable pedigrees



FIG. 78. Radiograph (Courtesy of Dr. W. B. Helm) showing a partial syndactyly in each hand of an individual. Some degree of webbing between the more distal portions of the affected parts is unusual.

of defects in man ever collected is one of this disease published by Nettleship. He succeeded in tracing the defect through nine generations, back to the seventeenth century. The genealogy includes 2,116 persons. The character behaves as a simple dominant in males, but frequently, though not always, females may be carriers of the defect in transmissible form though not exhibiting it themselves. That is, males in which the condition is simplex (Aa) develop the defect but females of similar simplex constitution (Aa) frequently do not. It follows, therefore, that normal males of such strains will have normal offspring but normal females may have affected children. In another family studied by Newman, night blindness was found to be inherited more after the manner of color-blindness, as a sex-linked character.

Other Traits Inherited as Dominants.—Not to go into details, other defects which behave as dominants or modified dominants in human inheritance may be mentioned. The following list is not complete and it must be understood that in some cases the statistics are insufficient to justify us in making anything but a tentative decision. We may thus enumerate as dominant over normality: *Achondroplasy* (abnormally short limbs with normal head and body); *Keratosis* (thickening of epidermis); *Epidermolysis* (excessive formation of blisters); *Hypotrichosis* (hairless, toothless condition); *Diabetes insipidus*; *Diabetes mellitus*; ordinary (not Gower's) *muscular atrophy*; *Glaucoma* (internal swelling and pressure of eyeball); displaced lens; *Coloboma* (open suture in iris); spottedness of hair-coat; corneal opacity; fragility of bones (*osteopsathyrosis*); abnormal outgrowths of bones (*exostoses*); beaded (*monilethrix*) hair; absence of lens of eye (*aphakia*); paralytic drooping of the eyelid (*congenital ptosis*); and lateral permanent incisors. Again studies have been made which indicate that the non-Jewish facial type is dominant to the Jewish; short, broad head (*brachycephaly*) to long head (*dolichocephaly*); pale, thick to colored, thin skin; feebly-inhibited temperament to over-inhibited temperament; and immunity to poison ivy seems dominant to susceptibility to it, though in this case the evidence is somewhat conflicting. The following conditions are probably Mendelian in behavior but dominance is imperfect or uncertain: harelip; cleft palate; extra teeth; defective hair and teeth; dental agnesia (absence of certain teeth); twinning; bilobed ear; cryptorchism; stiffening of the joints (*ankylosis*); and degeneracy of the cornea.

As a final illustration of a serious malady in man which acts as a dominant in inheritance, let us take *Huntington's chorea*. Ordinary *chorea*, or St. Vitus' dance, a disorder characterized by involuntary muscular movements, is commonly though not always confined to children and usually ends in recovery, but *Huntington's chorea* appears typically in middle life and is a much more dangerous malady. Fig. 80, below, represents the family history of one of five cases which have been studied by Doctor Lorenz in the Mendota Hospital for the Insane. All charts which have been platted of this malady show it to be inherited as a dominant. This means that half of the children

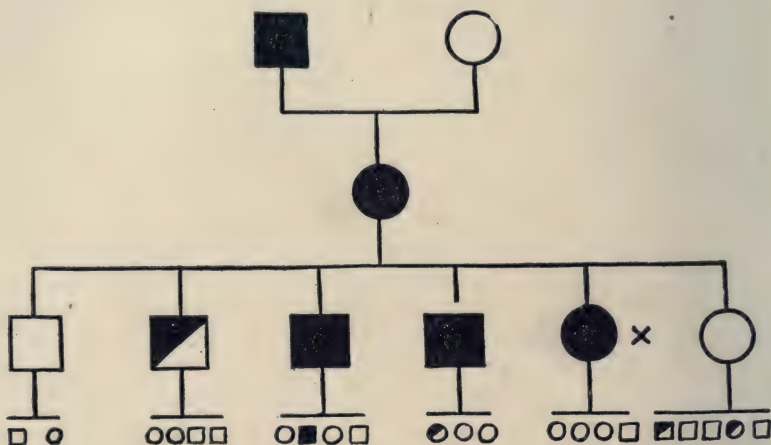


FIG. 80

Chart showing descent of *Huntington's chorea* in the P— family (courtesy of Dr. W. F. Lorenz). Squares represent male, circles female; shaded figures are choreic members of the family; partially shaded figures, slightly affected or very "nervous" members. The members of the last generation are for the most part still too young to show their condition. The cross indicates the individual in the asylum from whom the record was traced back.

of an individual who carries the malady in the simplex condition, and all the children of one who carries it in the duplex condition, are probably marked for this end. Fig. 81, p. 211, is another chart showing inheritance of *Huntington's chorea*. In still a third case at the Mendota Hospital, the gravity of the situation can be appreciated when one realizes that the patient

is the father of ten children, ranging in age from one to seventeen and one-half years. The calamitous fact that this disease does not manifest itself usually until middle life makes it likely that these children will all reach maturity, marry and in turn probably produce offspring before the doomed members of the family realize their fate.

Baldness.—According to the studies of Miss Osborn baldness is dominant in men and recessive in women, or in other

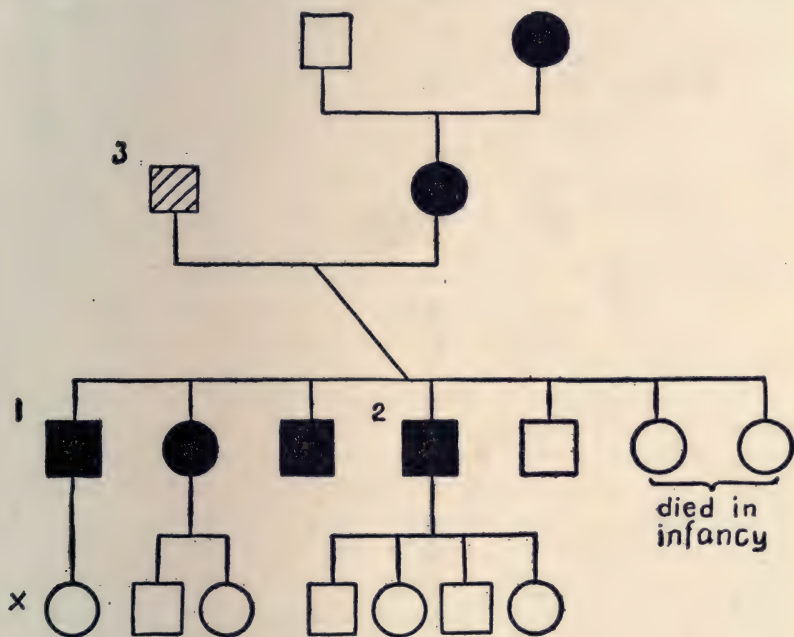


FIG. 81

Chart showing inheritance of *Huntington's chorea* in the R— family (courtesy of Dr. W. F. Lorenz); 1, 2 have been patients at Mendota Hospital for the Insane; 3, died of "paralysis"; the fourth or last generation indicated by the cross, ranging in age from 6 to 14, are too young yet to show their condition as regards this malady.

words men are bald if one factor for baldness is present but women are not bald unless both factors for baldness are present. Since fathers may transmit the factor for baldness to their sons as well as to their daughters the character is not sex-linked. Baldness, furthermore, commonly exhibits the same pat-

tern in a family strain. According to Miss Osborn, disease of the scalp or other environmental factors cause baldness only when the hereditary factor is present.

CASES OF RECESSIVENESS IN MAN

Recessive Conditions More Difficult to Deal with Because They are Frequently Masked.—Coming now to the question of recessive conditions in man, we find that defects are more likely to be of recessive than of dominant type. Apparently normality usually means the presence of normal genes and abnormality, the absence of some essential determiner. In the latter case, a unit-factor has seemingly been lost out or incapacitated in some way in the germ-plasm, and the product of such germ-plasm is therefore incomplete. As long as the loss is counterbalanced by the presence of a gene from the other line of ancestry, that is, as long as the simplex (Aa) condition prevails, the loss may not be in evidence, except in cases of incomplete dominance (taints, etc.), but any mating which permits of the production of the nulliplex condition will bring the defect to expression again.

The obscure nature of recessives makes such conditions more difficult to deal with than dominant defects. For as regards the latter we have seen that marriage of unaffected members of the family as far as that particular trait is concerned, is perfectly safe, even to a cousin, for once the germ-plasm is purged of such a positive factor, it, in so far as we know, remains pure. But in the case of a recessive character due to the lack of some necessary determiner a normal offspring of simplex constitution (Aa) will probably transmit to half of his children the capacity for handing on the defect, or if mated to another normal individual of simplex constitution (Aa) is likely to have the actual defect revealed again in one-fourth of his children and latent in two-thirds of the remainder.

Albinism a Recessive.—As an easily understood illustration of this type of case we may take human albinism, a condition which is due to the absence or inactivation of a pigment-developing gene. The albinic condition is recessive to normal condition. If albino (aa) is mated with albino (aa) nothing but albino children may be expected. An albino (aa) mated with a normal individual will have normal offspring (Aa), but they

will have the capacity for transmitting albinism to their descendants. Thus the normal offspring (Aa) of an albino (aa) and a normal parent (AA) if mated to another normal individual (Aa) who has also had an albino parent will probably transmit actual albinism to one-fourth of his children and the same capacity that he himself has of producing albinos, to one-half of his children, although the latter will appear to the eye to be normal.

Other Recessive Conditions in Man.—If for albinism we substitute certain forms of insanity, hereditary feeble-mindedness (Fig. 82, p. 214), or hereditary epilepsy, all of which apparently follow the same law, we can readily understand how unfit such matings are where both strains are affected. Marriage with similarly defective stock will result in the affection appearing in one-fourth of the progeny, and one-half of them, though apparently normal themselves, will have the capacity for transmitting the imperfection. It is in the existence of such hidden factors that the chief danger in the marriage of cousins, or in fact in any consanguineous marriage lies.

Some of the various defects which seem to be inherited as recessives when mated with normality are: susceptibility to cancer; *chorea* (St. Vitus' dance); true dwarfism (all parts proportionately reduced); *Alkaptonuria* (urine darkens after passage); alcoholism and criminality, where based on mental deficiency; hereditary *hysteria*; *multiple sclerosis* (diffuse degeneration of nervous tissue); *Friedreich's disease* (degeneration of upper part of the spinal cord); *Merriere's disease* (dizziness and roaring in ears); *Thomsen's disease* (lack of muscular tone); hereditary *ataxia*; possibly the tendency to become hard of hearing with increased age; certain forms of deaf-mutism; *paranoia*; *involutional melancholia*; alcoholism (where based on hereditary factors); tendency to bronchial asthma; degeneration of *macula lutea*; hereditary tremor; various forms of paralysis; enlarged eye (*megalophthalmus*); *pernicious anemia*; *cretinism*; *splenic anemia* with enlargement of the spleen; stammering; nosebleed (*epistaxis*); *chlorosis*; and predisposition toward such maladies as cancer, pneumonia, hernia (both inguinal and abdominal), spasmodic croup, some forms of jaundice, *arthritis deformans*, *arteriosclerosis*, curvature of the spine (*scoliosis*), *angio-neurotic edema*, gout, certain forms of rheumatism, migraine, goitre and exophthalmic goitre. Furthermore, studies have been made which

indicate that artistic ability is recessive to non-artistic; left-handedness to right-handedness; ambidexterity (probably) to right-handedness. Apparently also either very great or very small intellectual ability is inherited as a recessive.

Breeding Out Defects.—Even though recessive defects occur in a stock, there is the possibility of diluting out the imperfection in successive generations if care is taken always to marry into a stock wholly free from it. For example, a normal individual carrying a recessive defect will bear the abnormality in half of his or her germ-cells. This means that when such an individual marries a normal, non-carrier, half of their children will be wholly normal (AA) and half will be carriers; normal but of simplex constitution (Aa). If now this generation, carriers and

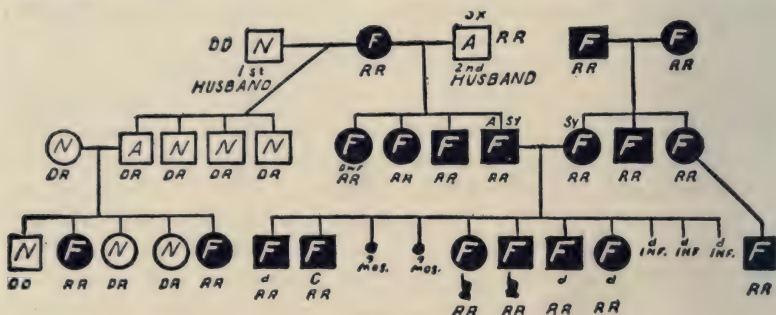


FIG. 82

Chart showing descent of feeble-mindedness as a typical recessive (after Goddard). Squares represent males, circles females; DD, homozygous dominant; DR, heterozygous dominant (i. e. normal although a carrier); RR, pure recessive; N, normal; F, feeble-minded; A, alcoholic.

non-carriers, marry only into normal strains of duplex constitution, then their combined issue will be likewise normal with only one-fourth of them carriers of the imperfections. This means that even if all of this last generation were married to persons having the defect only one out of four would have children showing it although the remaining children would be carriers. On the other hand if mated to normals only one-eighth of the next generation would be carriers. Thus by continually marrying into strong strains liability to manifest any recessive defect can be diminished in a few generations until the descendants are no more likely to have defective children than are members of our ordinary population.

Tuberculosis.—To what extent susceptibility to tuberculosis is a matter of heredity as against environmental factors is by no means clear in the case of man, although there is little doubt that hereditary non-resistance is an important consideration. Experiments on guinea-pigs and others mammals conducted by Wright and Lewis show that in such animals there are great differences in resistance to tuberculosis. They were able to isolate highly resistant as well as very susceptible strains which tended to breed true. Where resistant and less resistant stocks were crossed resistance appeared to be dominant although not in a simple, monohybrid way. Their results indicated that two factors for susceptibility were present, that the causes might be different in the two parents and that probably some three or four different factors for resistance might be involved in the different strains studied. As a result of their experiments they computed that about 60 per cent. of the differences were due to environment, 10 per cent. to such factors as age, weight and the like, and 30 per cent. to heredity. The factors responsible for resistance were apparently independent of those which determined general vigor.

In man apparently while almost any individual may contract tuberculosis when in a state of depressed vitality, or under stress of adverse surroundings, there is no doubt that certain families are more easily infected than others and much less resistant to the ravages of the disease when once it gains a foothold. However, a predisposition is a vastly different thing from the inheritance of the actual disease. For just as we are born with a nose well adapted to eye-glasses but not with eye-glasses on our nose, so many of us are born tuberculizable though not tuberculous, and every sanitary advance we make toward lessening the chances of infection is just so much more insurance for the susceptible.

The whole problem of tuberculosis is an extremely complex one. We do not know just the measure of the inheritance of the predisposition. Some writers in the past have maintained that tuberculosis is mainly a question of infection and not of inherent susceptibility, but steadily increasing evidence all points the other way.

Davenport asserts that in southern California a sub-race which is non-resistant to tuberculosis and bronchitis has been practically segregated. From a statistical study of tuberculosis made

on the English upper classes Pearson found a correlation of 0.50 between parents and offspring—the same as for physical traits—whereas the correlation between husband and wife was only 0.24, and even this, Pearson thinks, is in fact due to assortative mating. From a study of tuberculosis in convicts Goring also found correlation of 0.50 between parent and children but none between husband and wife. If tuberculosis were merely a matter of infection and not of innate resistance, it is argued, the correlation between husband and wife would be the same as that of parent and offspring, since the whole family lives under practically the same conditions.

Where the predisposition exists the chances of infection are still, even under the conditions of present-day sanitation, very great. The close association between a consumptive and other members of the family through a prolonged period of time, of course, renders the latter likely to infection unless unusual care is exercised. Very often if a parent is tuberculous a child contracts the malady shortly after birth and is particularly likely to do so if the mother, who nurses it and cares for it most intimately, is the tuberculous member of the family. Where the mother is tuberculous, indeed, the probabilities are that the child has already before birth had its vitality lowered through the toxins circulating in her blood or through defective nutrition, and in consequence does not resist well any diseases.

Undoubtedly a large proportion of our infant mortality is of tubercular origin. It is now a well-established fact that much tuberculosis in children is attributable to drinking milk from tuberculous cows, yet we find individuals so uninformed and dairymen so mercenary that they fight all attempts of the commonwealth to test out cattle for tuberculosis so as to condemn the infected individuals and thus save our babies. Investigations made in some of our large pork-packing establishments also indicate that hogs, especially such as have been around tuberculous cattle, are often shot through and through with tuberculosis and that such flesh when used as food, if not thoroughly cooked, may become a serious menace to our health.

With the wide prevalence of bovine and human tuberculosis it is little wonder that nearly every human being becomes more or less infected at some period of life. Autopsies on large numbers of individuals in some of our great hospitals have shown that as many as ninety-nine per cent. of the subjects show

tubercular lesions of some kind. While it is true that the class of people who would come to autopsy in such public hospitals would perhaps be more likely to be tuberculous than the average of the community, still it can not be denied that a very large degree of infection exists. Pearson, from statistics gathered in Europe, has shown that about eighty to ninety per cent. of the population have tubercular lesions before the age of eighteen. Hamburger found that in Vienna ninety-five per cent. of the children of the poor, between twelve and thirteen years of age, were infected with tubercle bacilli and he estimates that all would be before maturity. According to Doctor Mott, pathologist to the London County Asylums, the insane between the ages of fifteen and thirty-five are about fifteen times as likely to acquire tuberculosis as the sane are.

Yet the mortality from tuberculosis, great though it be, is obviously not in proportion to the enormous degree of infection. The crux of the situation is mainly the matter of resistance. From the standpoint of heredity, therefore, the question largely resolves itself into one of the inheritance or non-inheritance of constitutional resistance. Some are predisposed to be non-resistant and hence succumb.

The work of Karl Pearson* and other more recent researches forcibly indicate that hereditary constitutional predisposition is one of the chief factors concerned in subjects who develop well-defined attacks of the disease. Yet we must not forget that there are degrees of susceptibility and that therefore a constitutional predisposition which might be of little significance under good average conditions of nutrition and sanitation might be insufficient under unfavorable conditions.

Before we can make any relatively accurate estimate of the exact degree to which the malady is based on inheritance we must have more data. Many difficulties beset the path of the investigator. In the first place, when one gets back a generation or two he finds that diagnosis was crude and uncertain; a given malady may or may not have been tuberculosis. The main error, however, was probably on the side of not recognizing it in mild or obscure cases. Then again the questions of virulence of the infection, of size and frequency of the dose, etc., are also complicating factors. Moreover, in very many cases

* *The Fight against Tuberculosis and the Death Rate from Phthisis*, London, Dulau & Co., 1911.

the infection is a mixed one and hence we are dealing with other factors than straight tuberculosis.

Two Individuals of Tubercular Stocks Should Not Marry.—

However, sufficient is now known of the inheritance of susceptibility to the disease that we can have little conscience toward the welfare of the race if we countenance the marriage of two individuals who come each of tubercular strains, and marriage of even a normal person into a badly-tainted strain, where the one married is tuberculous, is extremely hazardous looked at from the standpoint of the children likely to be born of such a union. The Supreme Court of New York and the New Jersey Court of Equity have each held that the fraudulent concealment of tuberculosis by a person entering into a marriage relation is ground for the annulment of the marriage.

Cancer.—Concerning the cause of cancer in man there is a wide difference of opinion, although the present tendency is unquestionably toward recognition of inherent factors which make for resistance, or for susceptibility in the presence of the exciting agent. Although "cancer families" occur, available statistical evidence on the incidence of cancer is not sufficiently accurate or extensive to render it of much value in appraising the various factors concerned. Some of the most reliable family records of cancer are probably those collected by Warthin in a university hospital population, with diagnosis based on histologic examination in many of the cases. In one of the most impressive histories, seventeen of the forty-eight descendants of a cancerous grandfather had died of or been operated on for cancer. Others of the forty-eight were still too young to manifest cancer at the time the study was made. In another family in which the paternal great grandfather had died of cancer and the father and mother were both cancerous, all of the six children died of cancer, as did the only grandchild. Warthin concludes:

"In the histories of cancer cases coming from the state of Michigan and examined at the pathological laboratory of the University, about 15 per cent. show a striking history of multiple family occurrence. When the difficulty of obtaining good histories is considered, this proportion is relatively high, and, on the whole, corresponds fairly closely with the percentage obtained by Williams. We must conclude, then, that a definite and marked susceptibility to carcinoma exists in certain families and family

generations. This family tendency is usually most pronounced when there is a history of cancer in both paternal and maternal lines. In such families there is an especial tendency for carcinoma to appear at an earlier age than in the forebears, and in these younger individuals the cancer usually shows an increased malignancy."

Wolff, after reviewing his extensive compilation of cancer literature, concludes that 11 to 18 per cent. of the cases of recent investigation show heredity to be a factor in predisposition to cancer. Levin, using rather limited data collected by field workers of the Eugenics Record Office of the Carnegie Institution, found evidence that resistance to cancer behaves as a Mendelian dominant character and that susceptibility is the result of the absence of such resistance. Little, working likewise on the family history records of the Eugenics Record Office, found an increased occurrence of cancer in persons with cancerous parents or relatives. Furthermore, the cancer was often of the same type, affecting the same organ in related individuals. On the other hand, Pearson, using for a mass statistical study the histories of patients in a large charity hospital, found no greater proportion of cancerous relatives in cancer patients than in patients with other diseases. However, as Wells remarks in an essay on the influence of heredity in occurrence of cancer, the layman's information about family history used by Pearson, gained from patients in such a hospital, is probably largely worthless, and Pearson himself is dubious about the conclusions to be drawn from his statistics.

In experimental animals, however, notably mice, there is good evidence of hereditary family difference in predisposition to cancer, and inasmuch as cancer in such animals is essentially the same disease apparently as cancer in man there is little reason to doubt that the same biologic laws underlie each. Loeb has shown that certain families of mice are free from cancer while other families living under the same conditions are almost 100 per cent. susceptible. He found different degrees of susceptibility in different strains although the incidence in any particular strain was remarkably constant. According to the studies of Little and Strong susceptibility to one type of mouse tumor with which they worked required the presence of two factors, while susceptibility to another kind required a third additional factor. Various other investigators have found likewise that the hereditary constitution of mice determines whether or not they

are susceptible to cancer. Several workers have shown that susceptibility to grafted tumors is determined largely by heredity. By far the most extensive studies made in the inheritance of cancer are those of Miss Maud Slye. In work extending over a period of thirteen years, more than 40,000 mice have been given careful postmortem examinations and at least 5,000 spontaneous tumors, mostly malignant, have been observed. Miss Slye has found that not only the incidence of cancer, but also the type and location, are influenced by heredity. Her studies unquestionably demonstrate a marked inheritability of resistance to cancer. She finds that these two capacities are transmitted as unit characters and she has been able to isolate strains which generation after generation would manifest the same specific neoplasm such as lung-tumor, carcinoma of the mammary gland, or the like. In crosses between non-cancerous and cancerous mice she finds the non-cancerous condition dominant. In the offspring of such carriers (heterozygotes) the usual twenty-five per cent. of recessives reappear after the manner of a simple Mendelian pair of characters.

Loeb believes that in man there are one or more inheritable factors which predispose toward development of cancer. In a mixed population where there is much crossing of family strains this tendency is probably equalized. In certain relatively pure, uncrossed populations, such as are to be found in part of Norway, different family strains give evidence of marked difference in tendency to cancer.

Blood Groups.—In the transfusion of blood from one person to another it was discovered that the mixture of the bloods of certain individuals produced a kind of clotting of the red corpuscles technically termed *agglutination*. It is because of this fact that careful blood tests must be made before a blood transfusion; the bloods of donor and recipient must not be antagonistic. In 1900 Landsteiner and Shattock, working independently, found that human blood falls into definite groups.

On the basis of the agglutinative reactions the blood of any individual may be classified in one of four groups. The blood of every one belonging to the same group is compatible. Agglutination results in certain cases because the fluid part (*serum*) of one blood contains a substance which reacts with something in the corpuscles of the other blood. Landsteiner found that there are two agglutinable substances, commonly designated as A and

B in the corpuscles. Of the blood groups, Group I contains neither A nor B, Group II is characterized by the presence of A, Group III by that of B, while Group IV contains both A and B. The serum of a given individual will agglutinate whichever one of the two substances, A or B, his own cells do not contain. Thus serum of Group I will agglutinate the corpuscles of II, III, and IV; serum of Group II will agglutinate the corpuscles of III and IV; serum of Group III will agglutinate corpuscles of II and IV, while serum of Group IV, since it contains both A and B, will not agglutinate the corpuscles of any of the groups.

Every individual retains his particular blood characteristic throughout life. Furthermore, as shown by von Dungern and Hirschfeld, the blood groups are hereditary, apparently after the manner of a Mendelian dihybrid. Thus if one pair of genes be represented by A and a and the other by B and b then Group I must necessarily be of genotype $aabb$; Group II might be either $AAbb$ or $Aabb$; Group III, $aaBB$ or $aaBb$; and Group IV, $AABB$, $AABb$, $AaBb$ or $AaBB$. An individual of genetic constitution $AaBb$ mated to one of similar constitution would yield the characteristic four phenotypes (like the four blood groups) in the familiar 9:3:3:1 ratio of the ordinary Mendelian dihybrid (Fig. 48, facing p. 142). Knowing the blood group of a child it is possible, therefore, on the assumption that two pairs of characters are involved, to state that a person of a certain group could not have been its parent. For example, if a child is of Group II ($AAbb$ or $Aabb$) and its mother is Group I ($aabb$), the father could not have been of Group I or of Group III ($aaBB$ or $aaBb$). Thus the use of the blood group might be of importance in certain cases of doubtful or disputed paternity. In a recent study (*American Journal of Physical Anthropology*, April, 1926) of blood groups of 200 families involving 1,095 members, Snyder, however, maintains that his own data as well as that of other investigators indicates that the blood groups are inherited as a series of three multiple allelomorphs (page 137) rather than as two independent pairs of factors.

In 1918 the Hirschfelds, working on the troops which had been poured into Serbia from various countries, observed that the four blood groups occur in different proportions in different so-called "races." In general, more individuals of the north European races are of Group II (having substance A) than of any other group; more individuals of certain races from Asia

and Africa are of Group III (having substance B) than of any other group. Races around the Mediterranean basin contain about equal proportions of A and B. The following examples are illustrative (in part from Ottenberg, in part from Snyder):

	Group I	Group II	Group III	Group IV
Danish	47.3	36.7	12.0	4.0
Swedish	33.5	51.0	10.0	5.5
English	46.4	43.4	07.2	3.0
Senegal Negroes	43.2	22.6	29.0	5.0
Chinese (Pekin)	30.0	26.0	34.0	10.0
North American Indian supposedly pure.....	91.3	7.7	1.0	0.0
Indians, white mixture	64.8	25.6	7.1	2.4
American white	45.0	42.0	10.0	3.0

No very definite conclusion can be drawn at present regarding actual racial relationships from blood-group data since occasionally a very small racial group, such as the Ainu of Japan, may show two fairly distinct types.

Cousin Marriages.—No arbitrary rule can be laid down regarding the marriage of cousins. The traits, desirable or undesirable, revealed in the offspring of such matings will depend upon the qualities, either latent or expressed, which are already present in the family stock. Such inbreeding, by bringing together like characteristics, tends to perpetuate particular traits more certainly in a given strain. If they are valuable, well and good, but if undesirable, if defect meets defect, the result may be disastrous. The greatest difficulty in deciding on the advisability of marriage between relatives lies in the fact that every individual carries in transmissible form innumerable latent characteristics as well as those which are evident. When two such concealed tendencies are brought together—a situation more likely to occur in cousin marriages than in matings between unrelated persons—they become fully expressed in the new individual.

Since mental deficiencies, epilepsy, various insanities, susceptibility to tuberculosis, and many other human ills are of the type which thus remain dormant in an unsound stock only so long as overruled by a normal inheritance from one parent, before consummating a cousin marriage one should scan the family pedigree with careful eye. There are few families which do not possess some undesirable hereditary traits, and if cousins decide to marry they should at least do so with a clear-eyed vision of the extra hazards they are imposing upon their children. The

children of a cousin marriage, however, where each parent was free from inheritable defects, revealed or latent, are no more likely to beget defective offspring than are any other individuals. See also the discussion of inbreeding, page 172.

II. OTHER INHERITABLE CONDITIONS IN MAN

While many pedigrees show beyond dispute that such qualities as musical ability, literary ability, memory, calculating ability, mechanical skill, longevity, peculiarities of handwriting, obesity and muscular strength, for example, are inherited, their modes of inheritance have not yet been sufficiently analyzed to express them exactly.

Longevity.—While many complicating factors enter into determining length of life, there is evidence that inheritance is not a negligible one. Material collected and analyzed by Alexander Graham Bell, Karl Pearson, Raymond Pearl and others agrees in indicating inheritance of longevity. Bell, from a study based upon the genealogy of the Hyde family, found that where both parents lived 80 years, 20.6 per cent. of the children lived to be 80; where only one parent attained the age of 80, 9.8 per cent. of the children reached that age; and if neither parent lived to be 80, only 5.3 per cent. of the children reached that age. When both parents lived to be 80 the average life span of the children was 52.7 years, whereas if both parents died under 60, the children lived on an average only 32.8 years. Bell found, furthermore, that if the father lived to 80 and the mother died under 60 the average life of the child was 42.3 years; but when the mother lived to 80 and the father died under 60 the average length of life for the children was only 36.2 years.

Stature.—Stature, like many other quantitative characteristics is the result of the cooperation of a number of factors, the relative importance and number of which are unknown. In inheritance different individuals probably receive different assortments of these, hence no simple formulation of hereditary behavior can be given. In general the children of two tall parents are usually above average height, but short parents may sometimes have some tall children, hence the indications are that factors for shortness tend to be dominant. Davenport, from measurements made on sitting height, length of femur, height of knee, and the like, believes that the length of head, neck, trunk,

and legs as hereditary characters are distinct from one another and are independently variable, and that stature is dependent on the sum of these. Castle, on the other hand, mainly from observations made on crosses of large and small breeds of rabbits, stresses general growth factors which similarly affect growth in all parts of the body. The two interpretations are not, however, necessarily irreconcilable.

Body-Build.—Here again as with stature one is dealing with a compound character in which such matters as weight, skeletal conformation, obesity, and the like—themselves complex characters—enter. In general, stoutness tends to be dominant over slenderness.

Head-Form.—Pearson found the coefficient of correlation for shape of head between near relatives to range from 0.44 to 0.54—a high degree of correlation presumably indicative of heredity. The studies of Dunn on the crosses of the broad-headed Hawaiians with the medium to long-headed Chinese found the broad-headed condition dominant. In general, short head has been recorded as dominant over long although breadth of head and length of head seem to be more or less independent characters. There is considerable evidence, however, that endocrine secretions and environmental factors such as nature of food and the like may influence the shape of the head so that our understanding of the inheritable characteristics concerned is far from satisfactory. The matter is one of much scientific importance since so many anthropologists use head-form extensively in distinguishing races of men.

Skin-Color in Man.—The various hues and shades of skin-color are due to relative proportions of white, black, yellow and red which are to be found in different races. The black and the yellow colors are due to pigments. The white races have a minimum of black (melanin) while the negro races have a maximum of it. The yellow pigment is most obvious in the so-called "yellow" races of Eastern Asia. In the negro races, although abundant, yellow is largely obscured by black pigment. The mulatto, in addition to showing an intermediate condition between the white race and the black as regards melanin pigment, also reveals more of the yellow.

In man, the skin-color of the hybrids between negroes and whites is often cited as a case of blending inheritance in contradistinction to Mendelian inheritance. The skin-color of the

mulatto of the F_1 generation is intermediate between that of the white and black parent. This same degree of intermediacy is commonly supposed to persist in subsequent generations, but as a matter of fact, careful investigation has shown that while mulattoes rarely produce pure white or pure black children, there is considerably greater range in the shades of color in the F_2 generation and subsequent generations than in the F_1 generation. This is exactly what one would expect of a Mendelian character in which several cooperating factors were involved. Indeed, Davenport, who has made extensive studies* on the inheritance of skin-color in man, has come to the conclusion that the case is really one of Mendelian inheritance in which several factors for skin-color are concerned. Even the skin of a white man is pigmented in some degree under normal conditions. Davenport has shown in the skin of both whites and blacks that there is a mixture of black, yellow and red pigments. He concludes that "there are two double factors (AABB) for black pigmentation in the full-blooded negro of the west coast of Africa and these are separably inheritable." Since these factors are lacking in white persons the intermediate color of an F_1 mulatto would therefore be heterozygous for pigmentation, and subsequent generations, following the laws for segregation where a number of factors are concerned, would show different degrees of color because of the varying combinations of factors.

Multiple Births.—That a tendency to twin production characterizes many family strains seems to be a well-established fact. In a recent statistical study of twinning Davenport finds that twins appear in certain fraternities about four times as frequently as in the general population. Furthermore, his data show that the hereditary influence of the father on twin production approximately equals that of the mother. Thus, of 355 births in families where the mothers were from twinning strains, 16 or 4.5 per cent. were twin births; while of 289 births in families where the fathers were of twinning heritage, 12 or 4.2 per cent. produced twins. From statistics of human births in Norway, Bonnevie found that 1.34 per cent. of births were twins. In one family strain, however, the percentage rose to 1.95, thus showing a marked tendency to inheritance. Dr. A. Peiper has recently published (*Klinische Wochenschrift*) a pedigree chart of a wom-

* *Heredity of Skin Color in Negro and White Crosses*: Publication No. 188, of the Carnegie Institution of Washington.

an of non-twinning antecedents who was married to a man who was a twin. To this husband she bore nine pairs of twins. In a second marriage, with a man who did not belong to a twinning strain, although she bore six children, each birth was single.

How the father can have a hereditary influence on twinning is problematical. Except in the case of identical or duplicate twins which are believed to be from a single egg, twins are supposed to arise as the result of the simultaneous release of two eggs. Davenport points out that there is evidence that double ovulation is much more frequent than would be inferred from the number of twins produced. Apparently the failure of one egg to be fertilized, or if fertilized, to develop, is the cause of this discrepancy between double ovulation and twin births. If some factor in the male gametes of certain individuals could contribute to the fertilization and survival of a greater number of such twin ova than would ordinarily occur, then it is obvious how a father might be instrumental in twin production.

From a study of Prussian birth statistics and records obtained in the United States birth-registration area, Zeleny finds an interesting mathematical relation between the number of twin and triplet births in man. Thus, if $\frac{1}{n}$ is the number of twin births, $\frac{1}{n^2}$ approximates very nearly the number of triplet births. For example, of 13,360,557 births in Prussia from 1826 to 1849, 1 in 89.1 was a twin birth and 1 in $(88.9)^2$, a birth of triplets. The corresponding proportions for the registration area of the United States in 1917, when 1,339,975 births were recorded, was, for twins, 1 in 93.1, and for triplets, 1 in $(93.0)^2$. Zeleny concludes that "triplets are produced by the coincidence of two independent processes occurring with equal frequencies." One of these gives rise to twins.

The most remarkable instance of multiple births known in man is probably that of a woman living in Cleveland, Ohio, recorded by Davenport in 1919. Coming of a family in which her mother and her mother's mother were reputed to have had only twins, triplets or quadruplets, she had twins by her first husband, then successively twins, triplets, twins and twins by her second husband. By a third husband, she had twins, then triplets, a miscarriage of triplets, then twins, followed by a miscarriage of quadruplets, then twins, next triplets, then quadruplets, followed within a year by a miscarriage of quadruplets and the next year a miscarriage of triplets—or a total of forty-two births

and miscarriages from the same mother. In this family the tendency to multiple births is known to exist in four generations.

Mental Traits.—When it comes to mental characteristics we face a tremendously complicated situation. So many factors both constitutional and environmental are involved and these in such varying degrees in different individuals, that no one yet has succeeded in giving more than a series of approximations or general estimates of what, in mentality and the various more or less specific mental attributes, is inherited and of what is mainly the outcome of early experiences and training. As is explained in Chapter XVIII, the very nature of psychic attributes is such that because of the experiential and memory factors involved in their formation one can not fail to recognize the great importance of environmental factors, and yet the inherent underlying structures—general physique, central nervous system, and sense organs—must also be fundamentally important. The social, esthetic, emotional and intellectual qualities prized by man are so flexible and so much a very part of his social environment that they have not the definiteness of physical characteristics. While it is sheer nonsense to maintain that all men have equal capacities for all things and that the reason why one person succeeds in one occupation and others do not is solely because of difference in opportunity, still the inherent factors involved in such human fitness are highly elusive and in the main undetermined. Because of the outstanding similarities in mental traits in many family strains, however, one is compelled to believe in the inheritance of a considerable degree of specialization in the underlying structure.

In the lower animals unquestionably such mental traits as wildness, savageness, timidity and the like are inherited. Both Castle and Yerkes have shown that in rats wildness is transmitted to the young of wild fathers and tame mothers even when such offspring are reared by the tame mother entirely removed from the father. Yerkes proved further that timidity, though sometimes difficult to distinguish from wildness, is likewise inherited in rats, as is also savageness. Coburn, from a study of crosses between wild and tame mice in three generations, using in all some 1,300 individuals, found inheritance of both wildness and savageness. With this and kindred evidence of inheritance of mental differences among lower animals before us there is no reason to doubt such inheritance in man.

Pearson and others, using statistical methods, have found that in respect to various mental traits the degrees of resemblance between children of the same parents agree closely with those which have been found for various physical traits (a correlation of about 0.50). The method used is commonly the calculation of likenesses between near relatives, such as correlations between brothers or between parents and children with that of those between individuals chosen at random. Francis Galton in his various books, *Hereditary Genius*, *Noteworthy Families*, *English Men of Science*, and others, establishes the fact that certain family strains produce men of great ability much more frequently than do others. Various other studies yield the same result.

Heredity and Environment.—To wrangle over the question of which is the more important, heredity or environment, is about as idle a procedure as to argue which is the more important, the stomach or something to put in the stomach. Man would soon come to grief without either. So, too, the question of human development is not one of heredity alone nor of environment alone; both are necessary and must work hand in hand. Dormant capacities must have proper environment to call them forth, but on the other hand no kind of environment can evoke responses if some degree of aptitude is not present.

Professor Thorndike undertook experiments with groups of school children of high and of low initial ability respectively to determine whether equal opportunity or equal special training would produce an equalizing effect in easily alterable traits such as rapidity in addition and the like. Without exception he found that at the end of such experiments, although both groups had improved, the superior individuals were farther ahead than ever, that equality of opportunity and training had widened rather than narrowed the gap between the two classes. Others who have made special studies on the causes of individual differences have come to the same conclusion: namely, that individuals differ widely by original nature and that similarity in conditions of nurture and training will not avail in deleting these differences.

Galton and others, from extensive studies based on English sources, have shown that notable achievements have run in certain families to a degree that is inexplicable on the basis of opportunity alone; it can be fully accounted for only by attributing much to superior inborn capacity. Doctor Woods has shown

much the same thing for certain families in America. Schuster and Elderton have proved that there is a high degree of similarity in scholastic standing between fathers and sons in Oxford. Professor Pearson's measurements of mental characters in brothers and sisters while at school show a high degree of innate resemblance in many cases and certain cases of decided contrast. Where contrasts exist in certain families they remain unreduced in spite of the similarity of environment, thus proving that environment is less operative in the final intellectual establishment of such individuals than are their inborn aptitudes. Even in twins, as Galton, Thorndike and others have shown, there is no tendency for similar education, home life and the like to render those originally different any more similar with advancing years. Heron found little or no correlation between the intelligence of school children and adverse physical conditions such as adenoids and poor nutrition which are supposed to retard mental development.

To the contention that a high degree of correlation between relatives showing superior ability does not necessarily mean that inheritance is responsible but that more likely it is due to the superior environment to be found in intellectual families, the reply is forthcoming that even in intellectual families there are many individuals of not exceptional ability and that if environment is the decisive factor, since the family environment is largely the same, there is no way of accounting for the lesser ability of such individuals. From the standpoint of innate constitution, however, our knowledge of the random assortment of chromosomes which occurs during the reductions of the germ-cells and of the chance combinations which take place at the time of fertilization, shows clearly why children of the same parentage do not necessarily have the same attributes.

Comparisons of Duplicate with Fraternal Twins.—In comparisons of *identical* or *duplicate* twins with ordinary or *fraternal* twins we have perhaps the best means of any yet found for gaining knowledge of the relative potency of heredity and environment. Identical twins, since presumably they come from the same fertilized ovum and therefore have duplicate chromosomes, are two individuals with identical heredity, whereas ordinary or fraternal twins are merely two individuals born at the same time of the same parents. The effects of different environments on identical twins and of the same environment on ordinary twins should show what power environment has to modify the

inborn characters of individuals. Coming from the same ovum, identical twins have a single placenta and are encased in the same fetal membranes while ordinary twins occur in separate sets of membranes. From an examination of the placentas and membranes in 1,157 twin births, Alfehld estimates that 15.55 per cent. of twins are of the identical type. Not infrequently identical twins tend to be mirror images of each other as, for example, the right hand is a reversed image of the left. Thus if one such twin has the right arm slightly shorter than the left, the other has the left arm correspondingly shorter than the right, or if one has a slight defect or peculiarity of the right eye the other has the same condition of the left eye.

To cut a long story short, all studies made upon identical twins concur in finding them remarkably prone to remain nearly identical in spite of all differences in environing influences that may be brought to bear upon them. They develop the same tastes whether it be for music, architecture, painting or what not; they continue to be of the same mental or mechanical ability; they usually have the same appetites for foods; their handwriting is similar; they often dream about the same person at the same time, and not infrequently about the same things, even when in different places; their emotional natures, likes and dislikes are similar; and they often show the same idiosyncrasies toward certain foods such as being made ill by banana, disliking cantaloupe, having an aversion to tapioca, and the like.

Fraternal twins, on the other hand, are no more alike than ordinary brothers and sisters. They continue to maintain their differences when reared under the same environmental and educational conditions instead of becoming progressively more alike as they would if environment were the determining factor in development.

The weak point in the evidence from human identical and fraternal twins respectively lies in our inability always to be sure which are and which are not identical twins. We assume that twins of the same sex who are strikingly alike are identical and that those which do not show close resemblance are fraternal twins. There is no way, however, of proving the matter in man, since ordinarily we know little or nothing of their natal, much less their prenatal conditions. The studies of Newman on armadillo quadruplets, all of which are known certainly to come from a single egg, however, shed much light, as regards physical

traits at least, on the degree of inborn resemblance to be expected in identical twins. In 115 sets of armadillo quadruplets, where 1 stands for exact correspondence, he found the coefficient of correlation for a considerable number of body characters to be .93. Since ordinary brothers or sisters or fraternal twins show a coefficient of correlation of only about 0.50, if this coefficient is much higher, certainly if it approaches 0.90 in twins, it is probable that they may safely be regarded as of the identical or duplicate type.

The more recent studies of Merriman (*Psychological Review*, vol. 33, no. 5, 1924) and of Lauterbach (*Genetics*, Nov. 1925) throw additional light on twin resemblance and in general bear out the findings of earlier workers. Merriman, from Stanford-Binet tests of 105 pairs of twins, teachers' estimates of 90 pairs, Army Beta tests for 76 pairs, and National Intelligence tests for 143 pairs concludes that: (1) Environment appears to make no significant difference in the amount of twin resemblance when young pairs are compared with old pairs; (2) twins suffer no intellectual handicap; (3) and that there are two distinct types of twins—fraternal and duplicate (identical). This last conclusion is founded on the fact that the correlations of twin pairs of unlike sex lie near that of ordinary siblings while the correlations of like-sex pairs, are significantly higher. This higher correlation of like-sex twins indicates that a certain proportion of them are duplicate twins.

Lauterbach, from a study of physical and mental characteristics of 212 pairs of twins (71 boy-boy pairs, 78 girl-girl pairs, 63 boy-girl pairs) finds that: (1) older twins show no greater degree of similarity than younger twins (thus indicating that heredity is more potent than environment); (2) like-sex pairs of twins show a greater degree of resemblance than unlike-sex pairs (indicating that some of the like-sex pairs are duplicate twins); (3) unlike-sex pairs show a degree of resemblance about equal to that of single sibs; (4) there seems to be no definite tendency among twins toward greater similarity in acquired traits than in natural ability, although the evidence is somewhat conflicting; (5) there is no evidence that twins are intellectually handicapped; (6) and that, as mentioned by Danforth, left-handedness is closely associated with twinning. Lauterbach's data show that at least 19 per cent. of twin pairs are composed of a right- and a left-handed individual.

Professor Karl Pearson has done more perhaps than any other individual toward attempting actually to measure the relative strength of heredity and environment. Numerous statistical measurements lead him to conclude that it is a conservative estimate to regard heredity as at least five or ten times as important as environment in the development of the individual. A vigorous defense by him of this position will be found in *Biometrika* for April, 1914. Starch, in his *Educational Psychology*, estimates that in general one's achievements are dependent from 60 to 90 per cent. on original ability and from 10 to 40 per cent. on opportunity and external circumstance. While it is probably premature to express the relative influences of environment and heredity with mathematical exactness, such data as has been amassed through actual quantitative measurement, as distinguished from the mere assertions of "environmentalists," tends to substantiate Galton's final conclusion that: "There is no escape from the conclusion that nature prevails enormously over nurture when the differences of nurture do not exceed what is commonly to be found among persons of the same rank in society and in the same country."

CHAPTER XIV

ORIGIN OF NEW CHARACTERS

Variations.—So far the resemblances of animals to progenitors have been emphasized. Another equally important truth, however, must not be overlooked; namely, that no two individuals are ever exactly alike. The chief interest in heredity, in fact, lies in the study of the inheritance of these very characteristics which mark off individuals one from another. It is obvious that such differences must have originated frequently in the past, otherwise there could not have been the advance in the complexity and diversity of living things which we know has taken place. It becomes necessary, therefore, to inquire into the nature, origin and inheritability of these differences, or of what the biologist terms *variations*.

Variations may occur apparently in almost any conceivable direction and in any part; they may be mental, physical, useful, indifferent, or even harmful. They may be in definite directions in successive generations or merely fortuitous; they may be qualitative or quantitative, transmissible or non-transmissible. Often even scarcely appreciable differences are found to be inheritable.

Man takes advantage of this variability of organisms and by choosing generation after generation forms which have heritable variations in a given direction he can within certain limits establish the type he seeks. He also resorts to the crossing of promising varieties to get desirable combinations. In this way by selection and cross-breeding all of our common domestic animals, most of our fruits and vegetables, and many of our flowers have been obtained. The original apple, for example, was a small inferior fruit akin to the wild crab-apple of to-day. The large number of varieties we now possess have been obtained mainly through cross-breeding and selection on the part of man. When the colonists first came to America they brought with them the varieties of apple which were standard in their native country but by 1817, when the first American fruit book was published, more than 66 per cent. of the varieties recommended for culti-

vation were of American origin; that is, they were forms descended from the original varieties which had been introduced but they had changed sufficiently through variation and cross-breeding to be considered new varieties. Fortunately, once a valuable combination of traits is secured in such plants as the apple, it can be perpetuated indefinitely by budding or grafting. The grower thus avoids the many undesirable or valueless recombinations which occur in such multihybrid forms when grown from seed.

Classification of Variations.—Variations as a rule are slight. It was with such ordinary variations that Darwin largely concerned himself. Occasionally, however, marked variations termed *saltatory variations* or *sports* appear. The persistence of such variations throughout succeeding generations is often remarkable. Since Darwin's time biologists have begun to scrutinize this matter of variation much more closely, and they find that we have to discriminate sharply between kinds of variations. Variations may be classified in different ways, depending upon the use to which we wish to turn our data. The matter of greatest importance to students of heredity is whether or not they are inherited. Variations may be classified very simply as to:

1. The location of the cause of the variation, whether in the germ or the body.
 - a. *Germinal variation.*
 - b. *Somatic variation.*
2. Whether the variation is one of a series which fluctuate about an average or is an abrupt difference.
 - c. *Continuous variations or fluctuations.*
 - d. *Discontinuous variations or mutations.*
3. Whether the variation is a progressive one in successive generations, or without any definite trend.
 - e. *Determinate.*
 - f. *Indeterminate.*

a.—*Germinal variations* are such as arise from changes in the germ-cells themselves. They are present in the germ when its development into the adult sets in, and are unquestionably transmissible.

b.—*Somatic variations* are modifications brought about in the organism by external influences during development or in adult life. In contradistinction to germinal variations they are often spoken of as "modifications," "somatic modifications," "acquire-

ments," or "acquired characters." The use of the word acquired in this sense frequently leads to confusion since a new character which appears in an individual as the result of a germinal variation is also, strictly speaking, something that has been newly acquired. The ambiguity may be escaped in a measure by using the term *somatic modifications* to designate these new variations in the organism that are not of specific germinal origin. Somatic modifications are induced by the surrounding conditions which we call environment. These include influences which arise from the use or disuse of parts, as well as food, climate, accidents and the like. Such external factors under average or normal conditions of existence permit or call forth a certain type or direction of development. By altering them we may often bring about changes in the individual, such as suppressions or distortions of parts, enhanced development of some particular part or even new structures or features. Whether or not somatic modifications thus acquired are inherited is a question of such importance that we must discuss it presently at some length.

c.—*Continuous variations or fluctuations* consist of a series of small abundant variations. They are represented by a little more or a little less of a given character. The extremes are connected by all degrees of transitional stages. Darwin regarded these as the "ever present materials" which may serve natural selection "as a basis for species transformation," hence modifications of this kind are sometimes called *Darwinian fluctuations or variations*. Most biologists, as the result of many breeding tests, have come to believe that such plus and minus variations around a mean are in the main evanescent differences due to mere circumstances of growth and that therefore they do not each have a separate germinal basis. As such individual increments are not separately heritable they can, of course, afford no basis for selection. Since discontinuous variations are frequently so slight in extent as to render them undetectable from fluctuations the only way to determine the true nature of a given variation is through breeding. If when tried out by breeding the slight modification proves to be a heritable character it is commonly regarded as a small discontinuous variation, if not, a mere fluctuation. Darwin himself did not discriminate clearly between continuous and discontinuous variation except as he recognized the very considerable changes manifested in sports.

d.—*Discontinuous variations or mutations* are regarded as

abrupt germinal variations which arise without the appearance of transitional stages. They seem to occur irregularly and less frequently than fluctuations, although they are by no means rare. Sometimes, though not necessarily, they are changes of considerable extent. Permanency is a characteristic; they breed true from the very first. Once established they do not fluctuate around the old parental average of the character but around a new average of their own. Such a mutation may arise simultaneously in a number of individuals or in only a single individual. Many biologists have come to believe that mutations are the only variations of importance in the formation of permanent new characters, or, looked at from the evolutionist's standpoint, in the formation of new species.

Mutation Theory of Evolution.—Although not the first to conceive of a theory of evolution through sudden, abrupt variations, Professor Hugo de Vries, a Dutch botanist, was the first to advance a mutation theory with sufficient body of experimental evidence back of it to gain world-wide recognition and very general acceptance. After a number of years of experimentation and observation De Vries came forward in 1901 with the assertion that new species arise suddenly and fully established from a parent form which may continue to live side by side with the new form. He drew his conclusions from the extraordinary variations he discovered in successive generations of the evening primrose (*Oenothera lamarckiana*) a species which he found growing wild together with two of its variants (*O. brevistylis*, *O. laevifolia*) about Hilversum in Holland. The parent species itself had probably originally been introduced from America. Year after year he planted seeds of *Oenothera lamarckiana* in his garden and while the majority of the seeds produced plants true to the parent form, others developed into what appeared to be new species—as many as seven in all. Each successive year some of the *O. lamarckiana* seed would yield two or more new species. These new species, moreover, bred true in the main. As exceptions some threw one or two of the other new species found in the descendants of *lamarckiana*, and more rarely, entirely different new species. The different new or “elementary” species, as De Vries called them, were sufficiently unlike to be readily distinguished and taxonomists of Darwin's day would probably have regarded them as distinct species.

The accompanying table (Fig. 83, p. 237) shows the mutations

which arose in eight generations grown between the years 1887 and 1899 from *lamarckiana* seed alone. The seeds for each generation were from self-fertilized plants of *lamarckiana*.

De Vries' experiments have been repeated by a number of botanists, notably MacDougal and Schull in America and Gates in England, and his observations have in the main been confirmed and extended.

Some investigators, however, maintain that *Ænothera lamarckiana* was a hybrid to begin with and that the supposed new species are really only Mendelian segregants from this hetero-

ÆNOTHERA LAMARCKIANA
Elementary Species

Generation	<i>gigas</i>	<i>albida</i>	<i>oblong- ata</i>	<i>rubri- nervis</i>	<i>lamarck- iana</i>	<i>nan- nella</i>	<i>lata</i>	<i>scin- tillans</i>
I (1886-87).....					9			
II (1888-89).....					15,000	5	5	
III (1890-91).....				I	10,000	3	3	
IV (1895).....	I	15	176	8	14,000	60	73	I
V (1896).....		25	135	20	8,000	49	142	6
VI (1897).....		11	29	3	1,800	9	5	I
VII (1898).....			9	0	3,000	11		
VIII (1899).....		5	I	0	1,700	21	I	

FIG. 83

Chart showing mutation in the evening primrose (*Ænothera lamarckiana*) as described by De Vries.

zygous ancestor. De Vries himself denies this and brings forward various arguments to the contrary, not the least important of which is the fact that *Ænothera* is normally self-fertilizing.

Davis, for example, who regards the supposed mutation in *Ænothea* as really a "dissolution of hybrids" has, by crossing *O. francescana* and *O. biennis*, produced a hybrid which because of its resemblance to *O. lamarckiana* he calls *Ænothera neo-lamarckiana*. This form, likewise, produces variants which, were their ancestry not known, might be regarded as true mutants.

Various of the new or "elementary" species of *Ænothera*, however, have different numbers of chromosomes and this indicates that more than mere Mendelian recombinations is at the foundation of at least some of the differences. It seems not improbable from the experimental work of such investigators as Davis that

crossings and Mendelian segregations may enter also as complicating factors in this particular case. The somatic number of chromosomes in *O. lamarckiana*, the parent form, is 14, but a giant form, *gigas*, is characterized by having 28 chromosomes, or in other words it is tetraploid instead of diploid. Other chromosome numbers in *Oenothera* have already been indicated (p. 198).

A full appreciation of De Vries' work can only be had by reading his two volumes on *The Mutation Theory*, together with the many papers of the past twenty-five years which constitute the literature of the "*Oenothera* problem." De Vries recognizes various kinds of mutations. Thus *progressive mutants* differ from the parent species by having gained one or more characteristics; *regressive mutants*, by loss of certain characters; *degressive mutants* are weak species incapable of perpetuating themselves in the state of nature; and *inconstant* mutants are those which do not breed true, but occasionally throw other mutants.

Since De Vries' work has become well known the "mutation theory" of evolution has met with wide acceptance. Its opponents do not disbelieve in discontinuous variations—the fact of the existence of these has been long established—but they would deny that mutations are the only kind of variations involved in evolution, or indeed, that they are the chief kind. However this may be, the facts that interest us most at present are that abrupt variations do occur and that they are as a rule markedly heritable. Well known examples which are frequently cited as mutations among animals are the "japanned" peacock; the Ancon sheep, a former breed of short-legged sheep; Merino sheep; albinism in man or lower animals; hornless cattle; tailless cats, dogs, poultry, etc.; hairless dogs; and a host of others. Even more numerous cases have been listed for plants.

e.—Determinate variations.—Some evolutionists believe they find evidence of progressive changes, controlled by influences the nature of which is unknown, which bring about certain definite lines or directions of evolution, or what they term *orthogenesis*. They find that some variations are apparently not fortuitous but tend to accumulate in certain directions. These changes are germinal and inheritable. Such variations are seen supposedly in various degrees of expression in different groups of closely related forms, as the "eye-spots" on the feathers of the peacock pheasants, or the wing-bars or checkering in various species of doves and pigeons. It is not uncommon to find, in

fact, that when arranged with reference to any one of certain characters, such as some feature of the color-pattern, the different related species in a comprehensive group seem to stand at different levels of progression in the expression of the feature in question. Since when so grouped the gradation in pattern is often as much in evidence between collateral kinsmen as between those of direct lineage, it seems legitimate to conclude that the bias toward a particular type of pattern is the product of fundamental protoplasmic peculiarities implanted in the group as a whole.

While the individuals of a large group which show some particular characteristic expressed in different degree can be arranged in a gradational series, it is obvious, of course, that this does not prove that the various expressions of the character in question arose thus sequentially, or even in any particular order. Nevertheless although we know nothing of the order in which the mutations occurred which make up such a pattern series, the very fact that certain characteristics of organisms can frequently be arranged as parts of a definite pattern or as steps in a general progress, would seem to indicate a germinal tendency toward particular types of variation.

f.—Indeterminate or fortuitous variations.—So-called indeterminate variations are apparently merely chance variations. They may be fluctuations or mutations. Darwin laid much stress on such variations; he considered them the chief material upon which natural selection is based. According to him, if they happen to be useful they help to preserve their possessor in the struggle for existence and thus insure their own perpetuation. He believed, moreover, that with selection generation after generation the average around which the expression of a given character fluctuates continually rises. The modern mutationist would deny that the original plus or minus limits of a fluctuating character could be sprung in the least by either artificial or natural selection. He would maintain that if an increase or diminution beyond the normal range of fluctuation is to occur it must be through a new mutation and not by the waxing or waning of an old one.

It is now recognized that mutations, large and small, will serve as readily—or because of their permanency even more readily—as a basis for natural selection and the consequent development of adaptations, as will the “fluctuations” of Darwin. As far

as the outcome is concerned it seems largely a question of whether it was attained, as it were, by mounting steps or by ascending an inclined plane.

It is now recognized that the abrupt variations termed mutations, need be neither conspicuous nor widely different from the parent type. Nor are they necessarily, as was once believed, of rare occurrence. During the few years of intensive study of *Drosophila* since 1910, when Morgan first discovered a white-eyed mutant in a pure culture of normal red-eyed flies, more than 200 mutations in this species have been discovered and studied—some of them so slight as to be imperceptible to the untrained eye, and others of great magnitude. Yet all, from their very inception, breed true to the new type. In practically every species of plant or animal kept under close observation for any considerable period of time mutations have been observed.

There is, however, this crucial difference between the conception of evolution based on the selection of fluctuations and that based on mutation. The first, or Darwinian type of selection, carries with it the implication that continued selection in a given direction, presumably in some way as a product of the selection itself, not only secures a steady rise of the average around which the fluctuations vary but also induces an extension of the maximal range of variation in the chosen direction. That the limits of variation found in a given population can sometimes be extended by selection is shown in such studies as those of Jennings on *Diffugia* (page 184), although how such selection operates on the individual genes, if it does so operate, is not clear. Mere selection of individuals can of course do nothing directly to genes. One would have to suppose presumably that such genes as are amenable to the influence of selection are themselves variable and that, furthermore, once started, they tend to go on in a particular direction when the opportunity is given them. In general, however, the rise of the average in a mixed population which may be secured by selection is probably accomplished by weeding out the strains in which the variations approach the opposite extreme. The range of variation is thus narrowed and the population as a whole comes to stand nearer the upper level (Fig. 68, p. 183). This level, usually at least, can probably only be sustained, not extended, by selection. To secure any further advance the experimenter—or nature, as the case may be—must bide the time when a new mutation occurs.

It is evident, however, that with all individuals of a population possessing a particular character near to what is its present maximal development for the group, a mutation which transcends this maximum is more likely to happen than if a large number of the population possessed the character in a lower degree of development. A population of giraffes, for example, in which all adults range in height from 18 to 20 feet and averaged about 19 feet would be more likely to throw additional mutants over 20 feet than would an equally numerous population which ranged from 12 to 20 feet and averaged 16 feet in height.

Some biologists, notably students of geographical distribution, maintain, however, that species formation may go on by continuous variation as well as by discontinuous variation, and insist that at least, in the words of Sumner, "the burden of proof rests upon those who contend that these two types of variation and inheritance are reducible to a single category, that of discontinuity."

Causes of Germinal Variations.—Although we know more about the general nature of variations and of their probable locations in the germ-cells than did Darwin, his assertion that our ignorance of the causes of variation is profound is as true to-day as it was when he made it. It is plain from our modern knowledge of genetics, that apart from the mere somatic fluctuation induced by environmental factors, two kinds of variability are recognizable: one, the outcome of recombinations of existing genes as observed in the Mendelian phenomena and in abnormal chromosome distributions; the other, the result of changes in the hereditary constituents themselves. The latter, in so far as we know, constitute the sole source of actually new characteristics. While at one time biologists attributed great importance to sexual reproduction as a basis of variation and the origin of new characters, our modern knowledge of genetics makes it appear very doubtful that absolutely new characters, or at least new genes, can be originated in this way; what seems to occur under such circumstances is merely a reshuffling or resorting of old characters. Although innumerable permutations and combinations of genes may be made which find new expression, and which may afford a valuable basis for natural or for artificial selection, still such a process is not creating genes of new characters in the germ-plasm. While the possibility that genes may sometimes combine or influence one another so as to form actual

permanent new characters can not be denied, the proof of such performance, unless the occasional non-disjunction of certain chromosomes after synapsis be regarded as an instance of this, is wholly lacking.

Although we are uncertain about the method of origin of new characters the fact remains that they do arise in abundance as abrupt mutations or otherwise and become a part of the permanent heritage of a stock. It is clear that sexual reproduction may be one important means by which a given new character which has arisen in one or a few individuals may become incorporated in the species at large. Through Mendelian combinations and segregations it would by cross-breeding be spread and gradually introduced into more and more strains of the general population.

In our ignorance of how inheritable variations do come to appear in offspring we merely fall back on the assertion that they arise directly as germinal variations. Some biologists would attribute them to the fluctuating nature of living substance in general. The instability of protoplasm is one of its striking characteristics. It is constantly being broken down and built up, or, in other words, undergoing waste and repair. Like all other protoplasm, that of the germ-cells must also undergo these metabolic changes and it is possible though not proved that in this give and take of substances small changes occur now and then in their constitution which find expression in the offspring as variations.

No biologist to-day, in the light of the evidence available from the fields of embryology, cytology and genetics, would question the conception that the materials of the germ-cells have been derived, in the main at least, from the oö sperm by a process of cell-division, for this is the obvious explanation of how hereditary traits already established are handed on. This fact, however, tells us nothing about the acquisition of new genes nor the modification or loss of old ones.

Have the genes in question come into existence through the intermediation of the body, and if so was the influence general or specific? Are they attributable directly or indirectly to the external physical environment? Have they arisen in the germ-cells as the result of internal constitutional changes which bear no direct relation to the body? Or are they the outcome of now one, now another, or of combinations of these agencies?

These are the fundamental questions which confront us and which are likely long to confront us.

That changes in or among the chromosomes themselves sometimes occur has been established although the causes of such changes are unknown. Occasionally, as already stated (page 198), the number of chromosomes has been found to be doubled. Such tetraploidy is characteristic of certain giant types. Triploid conditions are also known in which only one of the haploid groups has been doubled. Then, too, instances of duplication of one or more chromosomes are known, due to the failure of the chromosomes in question to separate after synapsis (*non-disjunction*) or to other conditions which bring about irregular distribution of chromosomes. As knowledge of the structure of chromosomes increases evidence is accumulating that they, in some forms at least, may be highly complex structures compounded of what were probably at one time independent elements and that occasionally irregular or unequal divisions of these parts may be responsible for permanent germinal changes. Müller has even reported an instance of the loss of a piece from the middle of a chromosome in *Drosophila*, attested not only by the disappearance of characters the genes of which theoretically should be located in the mid-region of a particular chromosome, but by an actual visible deficiency in the specified region of the chromosome itself.

The frequent occurrence of polyploidy in plants is surprising. It has been found in many genera of wild plants including roses, maples, chrysanthemums and the jimson weed, as well as in such cultivated plants as wheat, oats, tobacco, sugar-cane, dahlias, mulberries, bananas and pineapples. In polyploidy the higher numbers have been built up by the addition of one or more complete haploid sets at a time, not by the gradual addition of single or a few chromosomes. Species are known in which an eight-fold (rose family, maple family) or even a ten-fold (docks, chrysanthemums) multiplication of chromosomes has thus occurred. Still other kinds of chromosome changes which have been discovered are end to end fusion of certain pairs in some species of *Drosophila* and transverse segmentation of all chromosomes in the primrose (*Primula kewensis*). Certain pairs of long chromosomes appear to have fragmented transversely in various genera of the lily family and the few large chromosomes in certain species of Japanese violets seem to have

been derived from the more numerous, smaller chromosomes of other species. Thus many of the constitutional changes in various species of plants have been found to be definitely associated with observable changes in the number or forms of the chromosomes.

In addition to such chromosomal modifications, however, there are changes in the individual gene. It has been established in *Drosophila*, for instance, that more than one change may occur at a single point in a chromosome. At the point where the gene for the "white-eye" mutation is located, for example, several other mutations have also appeared, producing true-breeding varieties in which the eyes are cherry, eosin, cream, or other colors. Lastly, it is known that a gene mutation may affect more than one character.

There is a general tendency among geneticists at present to restrict the term mutation to *gene* mutations, that is, to changes in the individual genes as distinguished from differences due to different assortments of existing genes. Since most of the so-called mutations in the evening primrose (*Oenothera*) are probably the result of redistributions of hereditary units already established, the resulting types are according to some geneticists more properly termed "variants" than "mutants." *Oenothera*, however, also exhibits some true gene mutations, the two best known of which are *rubricalyx* (dominant in crosses) and *brevistylis* (recessive). It is obvious that gene mutations rather than redistributions of existing genes are the changes of fundamental, creative importance, since they alone make possible the unitary differences that can be assembled in new proportions or combinations. The finding by Blakeslee, Bauer, Emerson, Maryatt, Zeleny and others of specially mutable factors in various organisms holds out the hope that in the near future more may be learned of the nature and rate of gene mutations.

CHAPTER XV

ARE SOMATIC MODIFICATIONS INHERITED?

Which New Characters Are Inherited?—Any new feature which appears in a given organism may have had its origin in some change which has come about in the germ from which it sprang, or it may be merely the product of some unusual stimulus operating on the body. While the outcome, as far as the present individual is concerned, is in each case a definite modification, the matter of inheritance is a very different question. On the first alternative where the new character is the outcome of germinal change, it is obvious that the altered germ-plasm will find expression in a similar way in succeeding generations as long as the new germinal combinations persist. On the other hand, if the new character has resulted merely from some special influence operating on the body of the individual, then to be inherited it would also have in some way to be transferred to and incorporated in the germ-plasm. Inasmuch as the body or soma of any individual is highly plastic and since various of its ultimate features may be mere somatic modifications, it is important to decide if possible whether or not somatic variations which are not of germinal origin can be inherited.

Examples of Somatic Modifications.—For example, the small foot of the Chinese woman of certain caste is the result of inherent germinal factor for the production of a foot plus the effects of binding which are in no wise germinal. The hand of the skilled pianist is a normal hand of germinal origin and normal environment plus the effects of special training. Again, the head of the Flathead Indian is a normal head of germinal origin and environment plus the effects of flattening. Similarly, almost any malformation of extrinsic origin may be cited, ranging from mutilations and amputations, scars and the like to monstrosities such as one-eyed fish which may be produced by subjecting a developing embryo to adverse conditions of development.

Use and Disuse.—Even reactions set up through the organism's own activities must produce changes. For example, a

muscle has a certain degree of normal development in the average man; it comes to this through the innate nature of its component cells plus an ordinary amount of exercise. It may, however, be developed far beyond this average by excessive exercise. On the other hand, it is a well-known fact that an unused organ weakens or may remain but partially developed. Thus either use or disuse may play an important part in the molding of a given individual. But whether or not in doing this it similarly affects the germ is a very different matter.

The Problem Stated.—The question is: can such enhanced or suppressed development, or can new or modified characters, produced in an individual by external agencies be so reflected on the germ-cell of the individual that they tend to reappear *as such* in its offspring without requiring the same external factors for their production?

Special Conditions Prevail in Mammals.—Before proceeding further we must recognize clearly the very special conditions which exist in most mammals. With them environment is in part an intra-maternal environment and in part independent of parental influences. Thus the formula for most non-mammalia would be—

Individual = egg + non-parental environment; but for most mammals, including man—

Individual = egg + intra-maternal environment + non-parental environment.

This condition in mammals introduces a complicating factor which is likely to obscure the whole issue unless we bear it constantly in mind. In man, for instance, we must discriminate sharply between two classes of influences which may exist in the infant at birth, or in other words, which are *congenital*; namely, those which were truly inherent—were in the germ-cells—at the very inception of the young individual, and (2) those which might later have been derived from either parent by the yet unborn offspring. The latter are not regarded as truly hereditary. Since certain diseases or their effects belong here we occasionally find a physician using the term inheritance for such prenatal influences, but the more careful ones now employ the term *transmission* to discriminate between such conditions and true inheritance. In its biological usage inheritance always refers to germinal constitution and

never to any condition that may be thrust on a developing organism before birth. It is clear, then, that congenital conditions are not all necessarily cases of inheritance.

Three Fundamental Questions.—To get at the question of the inheritance of body modifications with the least confusion, let us examine it in the form of three fundamental questions, as follows:

1. Can external influences directly affect the germ-cells?
2. Can external influences, operating through the intermediation of the parental body, affect the germ-cells? If so, is the effect a specific and a permanent one which persists in succeeding generations independently of external influences similar to those which originally produced it? Only such a condition as this would rank as the inheritance of a somatic modification.
3. Can the appearance of new characters be explained on any other ground, or on any more inclusive basis, than through the transmission of somatic acquirements, or do organisms possess heritable characters which are inexplicable as inheritance of such modifications?

Obviously the only way the question can be settled is through careful experimentation in which all possible sources of error have been foreseen and guarded against.

External Influences May Directly Affect the Germ-Cells.—There is evidence that under special conditions external influences may in certain organisms affect the germ-cells, but that this occurs commonly is extremely doubtful. For example, Professor MacDougal, by treating the germ-cells of the evening primrose with various solutions, such as sugar, zinc sulphate and calcium nitrate, apparently succeeded in producing definite germinal mutations. He injected the solution into the ovary of the flower the forenoon of the day at the close of which pollination would occur. He reports that in this way changes were produced in the germ which found expression in new and permanent characters.

Professor Tower experimented for a number of years with various species of *Leptinotarsa*, the potato beetle. By varying the conditions of temperature, humidity and atmospheric pressure when females were laying their eggs, he reports having produced variations in the young which came from these eggs although the mothers themselves were not changed. According to Professor Tower slight increase or decrease in these environ-

mental factors stimulated the activity of the color producing ferments, giving rise to melanic or darker individuals. Greater increase or decrease, inhibited them and produced albinos. He found also that at times the same stimulus might show different results in different eggs. The effect, therefore, is a general and not a specific one. Ordinarily the eggs of these beetles are laid in batches. When one of these batches was laid and left under normal conditions, the usual form of young hatched from it, but other batches from the same female under abnormal conditions resulted in the production of atypical forms. For example, a normal two-brooded form became five-brooded. The commonest modification was the production of various color types. These once established, according to Professor Tower, behave as independent, inheritable units. Still other experiments indicate that unusual conditions of temperature, food, moisture or the like may affect germ cells so as to produce general and indefinite modifications in offspring which are inheritable but this, of course, is very different from the inheritance of a particular change which was first induced in the parent body. Thus Blakeslee produced mutations in *Datura*, the jimson weed, by exposing parent plants to cold at flowering time. He believes that low temperature induced changes in the chromosomes of the gametes.

The experiments of Doctor Bardeen with X-rays and of others with X-rays, radium and other agents on the sperm and ova of amphibia and other animal forms show that the gametes are very susceptible to injurious influences at or near the time of fertilization. Thus Gee produced defective fish embryos by fertilizing normal eggs with spermatozoa which had been exposed to alcohol.

Influence of X-Rays and Radium.—There is considerable body of evidence which shows that chromosomes are susceptible to the influence of X-rays. Mavor has shown that exposure of the female fruit fly to X-rays while oogenesis is in progress may cause the elimination of the X-chromosome from the egg or bring about the inclusion of two X-chromosomes in one egg. When such eggs, characterized by irregular distributions of the chromosomes, are fertilized they develop into individuals which are exceptional in their characters and the exceptional condition is inherited. Mavor presents statistical findings to show that X-rays may modify the "crossover" values (page 192) between

chromosomes. The same dose may diminish the amount of interchange in the first or X-chromosome pair and increase it in the second. Furthermore the effects are not the same in the different parts of a chromosome pair. Since the exceptional flies which develop from X-rayed eggs are apparently normal in every way except their hereditary behavior Mavor maintains that his experiments show "a very clear case of an external agent which modifies the mechanism of inheritance in such a way that a permanent effect is produced which is transmitted through successive generations."

Little and Bagg found in the F_2 or later descendants of mice, which had been given light exposures of X-rays, that leg and foot deformities, eye defects, extreme short-headedness due mainly to jaw abnormalities, and changes in the length of hair on the flanks appeared, and that they were inherited in general after the fashion of Mendelian recessives, although the defectiveness varied much in amount and kind. These investigators while extremely cautious about expressing an opinion believe apparently that the abnormalities resulted directly or indirectly as a result of the X-ray treatment. One of the defects (jaw abnormalities) also appeared in their control mice not treated with X-ray. Snyder, on the other hand, failed to obtain any abnormalities in the 1,024 descendants from 50 male rats which had been previously irradiated with X-rays. In another experiment Bagg found that the uterine young of pregnant mice may be markedly affected by radium emanation. Some few of those born alive may mate and transmit eye defects, abnormal appendages, brain defects and the like though the effect seems to be general rather than specific in nature as regards inheritance.

Poisons in the Blood May Affect the Germ-Cells.—Any poisonous material in the blood or lymph might injuriously affect the gametes. We know, in fact, that such poisons as alcohol, lead and various drugs, and also the toxins of various diseases, do so affect germ-cells. Possibly the results of Doctors Harrison and Garrett who believe they have secured an inheritable form of melanism (black pigmentation) in Lepidoptera by feeding lepidopterous larvæ on foliage impregnated with lead nitrate or manganous sulphate, are to be interpreted in terms of such poisonous influences. Larvæ from such black strains when fed on pure food continued to produce melanic specimens. Moreover, the induced melanism was apparently inherited as a

Mendelian recessive. It seems plausible to suppose that changing condition of nutrition may affect the constitution of the germ-cells and thus induce changes in the organism which arise from these cells, but such nutritional effect is not yet a matter of established fact.

Difficulty of Explaining How Somatic Modifications Could be Registered in Germ-Cells.—As to our second query concerning the possibility of affecting the germ-cells through the intermediation of parental tissues, it is evident at a glance that since the germ-cells are built up along with the body and are not a product of it (Fig. 2, p. 11), if such effects are possible they must take place through the agency of some transporting medium. The germ-cells, being lineal descendants of the original fertile germ or zygote, already have the same possibilities of developing into an adult that the zygote had, and so the problem becomes one of modifying a complete germ already organized rather than of establishing a new germ by getting together samples of every part of the body. This is all the more evident when one realizes that usually the germ-cells are set apart long before the body becomes adult, that is, before the body has developed most of its characteristics. Moreover, among lower animals many instances are known where the immature young or even larvæ will produce offspring which nevertheless ultimately manifest all the structures of the adult condition.

But supposing specific modifications of the germinal mechanism were possible, it is difficult to comprehend how an influence at a distant point of the body could reach the germ-cell, to say nothing of the even greater difficulty of understanding how it could become registered in the germ in a specific way as affecting a particular part. For it must be remembered that the organs of the adult do not exist as such in the germ but are present there only as potentialities. How, for example, can a change in the biceps muscle of one's arm be registered in a germ-cell in which there is no biceps muscle, but merely the possibilities of developing one? Or how can increased mental ability which is contingent on the elaboration of certain brain-cells be impressed on a germ which has no brain-cells but only the capacity under certain conditions of producing such cells? For the brain of a child is not descended from the brain of his parent, but from a germ-cell carried by that parent.

On the other hand, it must be borne in mind that any organ

of the body is, after all, an assemblage of cells; each as much a lineal descendant of the original fertilized ovum as the most immaculate germ-cell, and as has been shown in the chapter on developmental mechanics, we have no reason to believe that somatic cells necessarily, any more than germ-cells, lose the hereditary potencies of the original zygote. If we are to make a just comparison, then, between an organ and the germ, it should be a comparison between the individual cells which compose that organ and the germ-cell. While various tissues may differ greatly in appearance, this is probably due mainly to cytoplasmic modifications or to the accumulation of intercellular products, that is, to differences in the formed products of the cell rather than to fundamental differences in the living protoplasm of the respective cells. It follows, then, that if changes in a given organ can release or engender products that operate specifically on certain elements in the component cells of that organ, such, for example, as a cytolytic agent, no undue strain is put on our credulity to suppose that, granted some sort of circulatory medium, these same products might reach and act similarly on the representatives of these elements in the germ-cells. In other words there is a conceivable path of connection, not wholly fanciful, between the vital constituents or genes of the tissue-cells and their distant brethren in the germ-cells.

Persistence of Recessive Factors.—In general; the persistence of Mendelian recessives is widely regarded as convincing evidence against the theory of possible somatic influence on inheritance. The inference is, that once such recessives become obscured, their factors should disappear if the body can influence the germ. But, granting somatic influence, one might well question why the factors for recessive should not persist indefinitely in the germ unless the somatic changes in question have some direct bearing upon them. This argument based on persistent recessives is somewhat beside the point. It would be valid against the old theory of pangenesis advanced by Darwin, which looked upon the new individual as an assemblage of samples collected from the tissues of the parent, but nobody advocates any such theory to-day. The idea that the constituents of the germ might be influenced by direct environmental conditions or by something transported to the gonad in the circulating fluids of the body is a very different one from the idea that the germ is constructed anew in each generation by aggregations of gemmules

from the various parts of the body. The one conception involves merely the modification of a mechanism already existing, the other implies recreation of an entire germ in each generation.

Transplantation of Gonads.—An interesting experimental test regarding the relation of the body to the germ was made by Castle and Phillips with guinea-pigs. It will be recalled from the discussion on Mendelism that when a black guinea-pig is mated with an albino the offspring are always black. These experimenters transplanted the ovaries from a young black guinea-pig to a young albino female whose own ovaries had been previously removed. This white female was later mated to a white male. Although she produced three different litters of young, six individuals in all, the latter were all black. That is, not a trace of coat-color of the white father or of the white foster-mother was impressed on the transplanted germ-cells of the developing young. The body of the mother seemed to serve merely as a protective envelope and a source of nutrition.

Convincing as this experiment seems at first sight, analysis shows that it is not conclusive. For black is dominant to white in crosses of black individuals with albinos, or in other words, when a factor for pigmentation is associated with a factor for albinism the former prevails. This being true, even if somatic inheritance were common, there is not the least reason for expecting a factor for albinism (and even less the *absence* of a factor for pigmentation!) to affect a factor for pigmentation in the implanted ovary, any more than in an ordinary breeding experiment we should expect albinism introduced by one gamete to affect the factor for pigmentation carried by the other gamete.

Effects of Mutilations Not Inherited.—Many experiments have been performed by investigators to determine whether or not the results of mutilation are transferred to succeeding generations, but so far only with negative results. Many such experiments have been unwittingly carried on for many generations, in fact, by breeders and fanciers, in the docking of horses, dogs and sheep, the dehorning of cattle and the like, yet no satisfactory evidence of the transmission of such conditions in any degree has ever been forthcoming. It is hardly to be expected, however, that a part removed from a body could affect genes in the germ-cells of that body even if somatic influence on germ-cells were common. The mutilations or distortions of the human body through various rites or social customs also fails to yield any

convincing examples of somatic inheritance. Foot-binding, head-binding, or waist-binding must be repeated in each successive generation to produce the particular type of "beauty" that results from such deformities. And lucky it is for man that injuries do not persist in subsequent generations, otherwise the modern human being would be but a maimed relic of past misfortunes.

Reappearance of a Character without Recurrence of Original External Cause.—For a new character to be regarded as an inherited somatic acquirement the demand is commonly made that it be capable of reappearing in successive generations without being called forth each time by the original causative factor. The idea is that once a gene is established in the germ it should maintain and express itself independently of the factors which engendered it. It may be questioned, however, if, without some qualifications, this is a just demand. Apart from the obvious exception that would have to be made for recessive characters in the presence of their dominant allelomorphs, there are certain adaptive characters which may have arisen as adjustments to a special environment which could scarcely be expected to reappear, in full expression at least, if the conditions to which such characters were adaptations no longer existed. It is a biological commonplace that an organ which is prevented from functioning remains underdeveloped or even atrophies, while one that is vigorously exercised, such as the muscles of a blacksmith's arms, may develop to an unusual degree. But even if, for example, the effects of muscular training were inherited it is evident that the new inheritance would not reveal itself unless the offspring of muscularly-trained parents performed at least a certain modicum of muscular work.

Certain Characters Inexplicable as Inherited Somatic Acquirements.—It seems incredible that some of the most striking features about certain plants or animals—such as so-called "passive adaptations"—could have been developed by means of the inheritance of somatic modifications, or at least of *adaptive* somatic modifications. For example, many animals such as the quail, the rabbit, or the leaf-butterfly are protectively colored. That is, they harmonize in color-pattern with their surroundings so closely that they are overlooked by their enemies. But how can this oversight on the part of an enemy so affect the bodies and through them the germ-cells of such individuals as to develop so high a degree of protective coloration? Or how,

indeed, could any of numerous adaptive structures which one can think of, such as the color or scent of flowers to lure insects for cross-pollination, the various grappling devices on many seeds to secure wide distribution by animals, or the like, have been directly produced by use or disuse or by any variation produced in them by the agents to which they are adapted?

On the other hand, it does not follow, of course, that because some hereditary characters can not have arisen from somatic modifications no hereditary traits could have thus arisen.

The Case of Neuter Insects.—A very instructive example of the improbability that great skill, highly specialized structures, or certain instincts are first developed in the parental body as the result of use and then passed on to the offspring, is seen in the case of neuter insects. In honey-bees, for instance, there are three classes of individuals: the drones or males; the queens or functional females; and the workers, which are neuter, that is, take no part in reproduction. The latter are really sexually undeveloped females. The queen can lay either fertilized or unfertilized eggs. The latter always gives rise to males. The workers gather the food, attend the queen, wait on the young, construct the comb, and in short perform all the ordinary functions of the colony except reproduction. They have many highly specialized structures on various parts of their bodies for carrying on their many activities, as well as the very highly specialized instincts necessary to the maintenance of the colony. But now, complex and highly developed as these workers are, since they do not give rise to offspring, no matter how much experience or structural modifications they may acquire during their lifetime, it can not be handed on to another generation. Nor can they have come to their present highly organized state through such a form of transmission since they are not the descendants of workers but of a queen. Any new inheritable modifications that appear in the workers of a colony must therefore have their origin in changes which have taken place in the germ-cells of the queen, and not in the soma of some other worker. It may be argued that the worker has not always been infertile; that at a more primitive stage of the evolution of the bee colony every female was both worker and mother; and that individual somatic acquirements might therefore have been transmitted; but this argument can not hold for many of the instincts or features of the modern bee because these have to do only with the condi-

tions of life which exist in the colony in its present form. It is obviously absurd to maintain, for instance, that all the highly specialized instincts incident to queen production, queen attendance and the like were functionally produced through usage before there was any queen to produce or attend, while on the other hand, the very necessity of queen production and maintenance is the outcome of the infertility of the workers. Some workers have been known to lay eggs, but as these are few in number and are never fertilized, which means if they develop they can only produce males, they can play no considerable part in inheritance.

Germinal Variation a Simpler and More Inclusive Explanation.—The foregoing constitute the main arguments against belief in the inheritance of somatic acquirements. Although when analyzed singly they are not as impregnable as the assurance with which they are usually expressed might lead one to suppose, taken all together, they unquestionably supplement one another and constitute a body of evidence which indicates that specific somatic acquirements are not commonly passed on to the germ. If such transfers do take place the occurrence is infrequent or at least inappreciable in one or a few generations. The gist of the whole matter regarding the source of new characters in offspring seems to be that the explanation based on the idea of germinal variation is in last analysis the simpler and more inclusive, and there are few if any alleged cases of inheritance of a parental modification which can not be likewise explained as the result of a germinal variation. There are numerous cases which can not be explained as transmissions of somatic acquirements even if this transmission could be established in certain cases. So, many biologists argue, why have two explanations when one is sufficient, especially when the other has never been conclusively established as true in any case and is obviously untrue in certain test cases?

It is well to remember, however, that amassing an array of negative evidence against one theory does not establish the truth of a rival theory. And successful as have been the opponents of the hypothesis of somatic transmission in showing the untenability of this view, they have been little if any more successful than its proponents in explaining satisfactorily how changes *are* initiated in the germ-cell. To say that new characters arise as the result of spontaneous changes in the germ, if by "spontane-

ous" is meant strictly self-generated, can have little or no meaning. If we mean by it germinal changes about the causative stimuli or external relations of which we know practically nothing at present, then perhaps it is permissible in our ignorance to use it as a convenient term.

In such a hand-and-glove relationship as exists between organism and environment, it would seem that directly or indirectly environment must play an important part in initiating, or at least in conditioning, changes. Time and again in the past, according to paleontologists, whenever new conditions arose which would permit of the existence of living organisms new forms of life admirably adapted to those conditions appeared. In some way the environment molds these new inhabitants to its bounds and it seems well-nigh incredible, no matter what eons of time are vouchsafed us, to believe that this has been done merely by the negative method of killing off generation after generation of the non-conformists. For on such a basis not only has the adapted organism had to await the accidental occurrence of a favorable germinal variation, but of hosts of them, often highly interrelated which then must be sifted and perfected by natural selection through innumerable generations to bring about that marvelous adaptedness to the environment which characterizes living things. Yet, on the basis of available evidence, such is the view to which we seem driven unless we suppose that there is some more direct principle of adaptation in living organisms which biologists have failed as yet to discover. This much is sure in many animals at least; we find abundant evidence of compensatory and other adaptive responses of the body initiated through the agency of the serological mechanisms of the organism. It would seem worth while, therefore, to seek in the same direction for light regarding the possible existence of some form of adaptive germinal impress. For when one perceives the many cooperative activities of the various parts of the body and how change in one part such as an endocrine gland may produce pronounced effects in the furthest reaches of the body, it seems improbable that the germ-cells bathed in the same fluids, nourished with the same food, stand wholly apart.

The attitude of most investigators is that of the open mind. While feeling that the weight of probability is very decidedly against the theory of inheritance of somatic modifications, they stand ready and willing to accept any evidence in its favor which when weighed in the balance is not found wanting.

The Problem Restated.—It may be argued, in fact it has been argued that anything which environment brings out is in a sense hereditary since the “makings” must already have been present in the germ-plasm before the finished character can be called forth. According to this interpretation what appears to be a newly acquired character is only the expression of unusual environmental influence operating on germinal predispositions already in existence. On such a basis there can be no somatic acquirement which does not already have germinal representation.

Is not stating the problem of heredity this way, however, on about the same shadowy basis as affirming that the potentia of the oceans, continents and topographical features of the world to-day were present in the original nebula which preceded our solar system, or that man lived potentially in some primitive protozoa-like creature? While in a sense this may be true the writer does not believe that the most optimistic of geneticists would expect to find the genes of man’s present manifold attributes in such primitive protoplasmic creatures.

What seems to have happened in the evolution of living things is that such originally indefinite “might-bes” have become the present “ares.” In other words, of the many possible outcomes inherent in the very physical and chemical nature of the vague initial life-substance, some have been realized. Furthermore, in the organisms of to-day this realization has progressed from the realm of indefinite possibility to a more or less specific certainty through the origination in cells of representative packets which we call genes. Through the action of these, subject to the existing environment, the characteristics of present-day forms are achieved. In other words, no matter how devious the path of procedure or how tangled the skein of chemical relationships, there is a certain determinate correspondence which did not exist in the primitive ancestral protoplasm, between special elements in the germ and the characteristics of the body as they are expressed to-day.

If this is untrue, then either there is no problem of evolution or it is wholly different from what it is commonly conceived to be. If it is true, then the great key problem of evolution—that of the origin of inheritable variations—is this very one of how the genes which exist in germ-cells to-day have been gradually incorporated in the erstwhile primitive protoplasm. This

accumulation, which most of us take for granted, has not been a mere hit-or-miss affair, moreover, but an orderly, sequential process. Each new acquisition has been possible largely because of some earlier acquisition. In an organism the past history of a part is an important factor in its present expression. Where once reigned possibilities which *might* be realized, there now exists a new, more specifically determinative mechanism which persists as the established constitution of the germ.

Non-Inheritance of Parental Modifications Has Social, Ethical and Educational Significance.—Like many other biological conclusions these relative to the non-inheritance of parental modifications are of extreme importance to humanity. It is clear that they have not only physical but social, ethical and educational significance. For if the education which we give our children of to-day, or the desirable moral conduct which we inculcate does not affect the offspring of succeeding generations through inheritance, then the actual progress of the race is much slower than is commonly supposed, and the advance of modern over ancient times lies more in an improvement in extraneous conditions through invention and the accumulation and rendering accessible of knowledge, than in an actual innate individual superiority. And when we face the issue squarely we have to admit that there is no more indication of the inheritance of parentally-acquired characters as regards customs, knowledge, habits and moral traditions than there is of physical features. In fact, if such acquirements were inherited then we should soon have a race which would naturally, spontaneously as it were, do what its ancestors did with effort. Yet we do not find the children in our schools reading, doing sums and developing proper social relations without ceaseless prompting and urging on the part of the teacher. Indeed I can testify that this necessity carries over even into a university. In short, the habits and standards of each generation have to be instilled into the succeeding generation.

No Cause for Discouragement.—At first glance when we realize that notwithstanding our individual advancement, that in spite of all our painstaking efforts toward self-improvement, we can not add one jot or tittle to the native ability of our children, that, aside from possible advantageous germinal variations, they will have to start in at approximately the same level as we did, and like us will have to struggle, or be coaxed, pulled or spurred

up to the higher reaches of attainments, we are apt to feel discouraged and to look on heredity as the hand of fate which irrevocably bars progress. But there is another side to the picture. This very fact of heredity which can not be altered at will is the conservative factor which maintains the excellence of our standard strains of plants and animals, and sustains man himself at his present level of accomplishment. While we are denied advancement through the efforts of the flesh, we are also largely protected from our misfortunes and follies, as witness the non-inheritance of mutilations, of various maladies of extrinsic origin, or of personally acquired bad habits.

Improved Environment Will Help Conserve the Superior Strains When They Do Appear.—If we can not hand on to our descendants a personally enhanced blood heritage, we at least can do our share toward building up a social heritage of established truth, of efficient institutions and of stimulating ideals, through which their dormant capacities may be led to expand more surely and more effectively to their uttermost limits. Each advance in such social heritage will tend more and more to create an atmosphere which will make it sure that the occasional real progressive and permanent variations which occur from time to time will find adequate expression and preservation in future lines of descendants. It will reduce the numbers of our "mute, inglorious Miltons" by more certainly disclosing the individual of exceptional talents and insuring for him an opportunity of revealing them to the best advantage. Above all, since surrounding influences are especially powerful on young and developing organisms, we should realize that great care must be exercised in behalf of the young child to secure an environment which is saturated with wholesome influences. For it is a rule of development that if the environment is faulty the organism is impaired.

CHAPTER XVI

ARE SOMATIC MODIFICATIONS INHERITED (continued)?

ANALYSIS OF CASES

While space will not permit extended discussion, in order further to fix the nature of the problem in mind as well as to exemplify the conditions that must be satisfied to form convincing evidence of inherited somatic acquirements, it will be well perhaps to analyze a few typical cases as they are frequently cited.

Experiments on Insects.—Many insects in the larval stages, particularly just after pupation, seem to be especially susceptible to external influences. They have been much used, therefore, for purposes of experiment. It has long been known that differences in size, in color and even in the shape of wings and other parts of the body can be produced by various agents if applied at this period of development.

It has been found that in some cases where male and female are of different color, the color of the female can be changed to that of the male by altering the conditions of temperature. In certain cases types can be changed by cold so that they resemble varieties of the same species found farther north, and by heat, varieties found farther south. But not all individuals of a given lot are affected, and often different individuals of the same kind show different effects. Moreover, in some cases the same aberrations are produced by heat as by cold. This indicates that it is not so much a question of specific effects as a general physiological change, apparently mainly a matter of direct influence of temperature on the chemical composition of the pigments. The Countess von Linden in fact has shown that the extracted pigments can be made to undergo the same changes of color in a test-tube by heat and cold as in the pupæ. But there is no evidence that the germ-cells of the living insect were affected in a specific way. In a small fraction of the offspring of such modified individuals abnormalities appeared, but these were not always of the same kind as those which had been pro-

duced in the parent. That is, there was no evidence of a trait or character having been acquired by the body and handed on to the germ-cell.

Size, colors and markings of butterflies have also been altered by subjecting the caterpillars or the pupæ to such influences as strong light, electricity, various chemical substances, centrifuging, diminished oxygen supply, etc., but the results were in the main confined to the immediate generations. In the few cases where permanent inheritable changes were seemingly produced they were more reasonably interpreted as the effects of direct action on the germ-cells than as examples of inherited somatic modifications.

Payne found that neither the size nor the functional efficiency of the eyes of fruit flies which have been bred in the dark for sixty-nine generations were impaired. Lutz likewise in an experiment intended to test the influence of disuse found no detectable diminution in wing length or structure in a strain of fruit flies bred for forty-three generations in narrow vials which prevented use of their wings in flight.

Starvation experiments which resulted in the dwarfing of adult individuals have been performed on various insects, and while the dwarf condition may persist through one or two generations due to a diminished food supply in the eggs of the dwarf, the stock in question when returned to normal food conditions soon resumes its original characteristic size.

Experiments on Plants.—Many experiments have been performed with plants, inasmuch as they are particularly prone to become modified by changes of food supply, or climate. For example, plants which grow luxuriantly in a warm moist climate or a rich soil may become stunted and markedly changed if transplanted to a cold climate or a poor soil. Naturally, their progeny will exhibit the same behavior as long as they are kept under the new conditions. Experiments carried on through numerous generations, however, practically all show that the germinal constitution of the plants remains unchanged, for when their seeds are planted under the original favorable conditions of soil or climate, the plants resume their former habits of growth. Naegeli, for instance, who made a study of many varieties of Alpine plants, and who carried on experiments with many of them for years in the Garden of Munich, concluded that no permanent effects had been produced by the Alpine climate and conditions

in plants from other regions which had come under its influence. A few botanists have found that the changes produced by the Alpine climate have persisted for a generation or two and have then worn off. More recent experiments on various of our field grains which have been stunted and cut down in productivity by growing for a number of generations under adverse conditions show that they have not been permanently modified by such treatment, for they resume normal productivity and size when grown again under favorable conditions.

On the other hand, Lederbaur found that a common weed, *Capsella*, when transplanted from an Alpine habitat to the lowlands did not return to the lowland type of the weed, but retained certain of its Alpine characteristics. It is not clear, however, that this particular species during its long sojourn of many generations in Alpine conditions may not have undergone a series of germinal variations and have developed into a new variety or species quite independently of changes wrought in the germ by reflected somatic effects.

Even when different plants are grafted together, as when a branch from one variety of fruit tree is grafted upon a tree of different variety, neither modifies the hereditary constitution of the other. The same is true of animal grafts.

Experiments on Vertebrates.—Although somatic modifications are easily produced in vertebrates, evidence of their inheritance can no more be unequivocally established than in plants or in invertebrates. Different kinds of amphibia subjected to marked environmental changes have manifested various modifications which have shown some degree of persistence, but in most of the cases recorded so far it is not clear that what has been accomplished is not the mere accentuation of constitutional conditions already inherent in the germ instead of the origination of new ones. Typical of these is the transformation of the aquatic, gill-breathing salamander *Axolotl* into the gill-less land form *Amblystoma*, heretofore regarded by systematists as a different species. Marie von Chauvin accomplished this by decreasing the amount of water in an aquarium. The experiment has also been repeated by others. Either of these amphibians when sexually mature produces its like. The salamanders in question have both lungs and gills, but after a time the ones which are to be land forms lose their gills and become exclusively lung-breathers. What seems to have been accomplished, then,

is the accelerating or forcing of normal natural tendencies already inherent in the organism instead of introducing something new into the inheritance by way of the soma. Axolotl is in all probability merely a larval form of *Amblystoma* which with high temperature and an abundance of water reproduces without advancing to the final possible stage of its life cycle.

Kammerer has made many experiments with amphibia and other animals in which he believes he has secured inheritance of somatic influences, but his book on *The Inheritance of Acquired Characteristics*, published in 1924, is disappointing because of the vagueness which enshrouds the more critical details of his experiments, his apparent lack of checks and controls, the possibility of more than one interpretation of the results, and his whole attitude of mind which is partizan rather than judicial. The following may be cited as a representative experiment.

Salamandra maculosa is a black-and-yellow salamander which lives in damp woods. It deposits in water a large number of young sufficiently advanced in development to be provided with gills. After several months they lose their gills and metamorphose into land forms. *Salamandra atra*, a closely related black Alpine species, gives birth to only two young at a time and these are completely metamorphosed and ready for terrestrial life at birth. Kammerer found that by keeping the black-and-yellow form from water he could force it to retain its embryos within its body until they were completely metamorphosed as in the black salamander. Furthermore the number of young at birth was greatly reduced and the color of the young was almost wholly black. These animals when sexually mature were given access to water, where they deposited their young. The young, however, were much further along in metamorphosis at birth than are ordinarily the young of the black-and-yellow salamander and they left the water in a few days instead of remaining there the customary few months. When the reverse experiment was tried on the black Alpine species it was modified toward the procedure of the black-and-yellow type, and there was likewise a partial persistence of the acquired mode of reproduction. Kammerer's book is full of suggestive experiments which, although unconvincing as they now stand, offer possibly profitable lines of attack on the question of somatic inheritance if performed under rigid control.

Temporary Effects of Environment.—Certain changes have

been produced in the germ-cells or in the embryos of various forms, which last for one or two generations and then disappear, but these should be regarded as nutritive, chemical or other influences which linger on for a time as after-effects rather than as changes in hereditary constitution. Whitney, for example, found that rotifers injured by alcohol became less resistant to certain poisonous salts, and less fertile, and that under normal conditions this depression persisted through one generation of offspring but disappeared in the second generation. Woltereck found that in *Daphnia*, a small crustacean, exposure to cold produced an after-effect which lasted a generation or two. Sumner showed that mice reared in the cold had shorter tails than those reared at higher temperature and that this modification reappeared in the next generation. Stockard found that defects may appear in the offspring of alcoholized guinea-pigs and persist for two or more generations (see page 292).

Are the Effects of Training Inherited?—Breeders and trainers very commonly believe that the offspring of trained animals inherit in some measure the effects of the training. Thus the increased speed of the American trotting horse is often pointed to as strong evidence of such transmission. According to W. H. Brewer, the earliest authentic record of a mile in three minutes was made in 1818. The improvement, approximately by decades, from that time was as follows:

During 1st	decade after 1818, improved to 2:34
2nd	" " " " " 2:31½
3rd	" " " " " 2:29½
4th	" " " " " 2:24½
5th	" " " " " 2:17½
6th	" " " " " 2:13½
7th	" " " " " 2:08½

By 1892, the date of Professor Brewer's publications (See *Agricultural Science*, Vol. 4, 1892) the record had reached 2:08½. Since then it has been lowered still further.

On the face of it this looks like a good case of inheritance of training, and Brewer himself believed it such. If so this would mean that colts of a highly trained trotter would be faster than they would have been if their parent had remained untrained. It is impossible to get positive proof in the case of any trained horse since there is no way of establishing just how speedy the progeny would have been had the parent remained untrained. If it could be shown that colts sired by a trotter

late in life were on the whole faster than those sired by the same father when younger and as yet not highly exercised in trotting, then the facts might give some evidence of value, but unfortunately no such records are available.

On the other hand, even ignoring the fact that improvement in track and sulky are probably the biggest items in the shortening of records in recent times, *selection*, instead of inheritance of the effects of training, will equally well account for any innate progress in trotting. And since, as pointed out by Professor Ritter, there are even more striking cases of similar improvements in other fields, such as college athletics, where the factor of use-inheritance is entirely precluded, it is wholly unnecessary to postulate it in the case of the trotter.

For example an inspection of the records of college athletics for the last thirty-five years in running, hurdling, pole-vaulting, jumping, putting the shot, etc., shows on the whole a steady advance year by year. Moreover, the greatest improvement has occurred in those events in which skill and practise count for most together with selection of the inherently ablest candidate for the events. But in the case of athletics the improvements shown in thirty-five years have all come within a single generation and hence the inheritance of the effects of training is ruled out as a factor. Selection and improved training are the only factors operative.

In the case of the trotter inheritance undoubtedly has also been a factor, but inheritance based on selection from what the race-track has shown to be the speediest individual, not inheritance of the effects of training. In other words, horses which have shown the capacity for being trained to the highest degree of speed have naturally been selected as sires and dams and so through selection generation after generation a speedier strain has gradually been established.

Instincts.—When we turn to the realm of mental traits, particularly of instincts, we meet with a host of activities which are frequently pointed to by transmissionists as examples of inherited acquirements. Thus according to them, habits at first acquired through special effort ultimately become instinctive, or according to some, instinct is “lapsed intelligence.” Instances often cited are the pointing of the bird-dog, the extraordinary crop-inflation of the pouter pigeon, or the tumbling of the tumbler pigeon. We can not stop to discuss these cases beyond pointing

out as many others have done that practically all dogs have more or less of an impulse to halt suddenly, crouch slightly and lift up one forefoot when they scent danger or prey, that all pigeons pout more or less, and that practically all show more or less instincts of tumbling when pursued by a hawk. Thus in all of these cases the fundamental germinal tendency is already at hand for the fancier to base his choice on and thus through selection build up the type desired. Just as in the fan-tailed pigeon, by repeatedly selecting for breeding purposes individuals which showed an unusual number of tail-feathers he has built up a type with an upright, fan-like tail having many more feathers than the twelve found in the tail of the ordinary pigeon, so by similar procedure in the case of other forms he has markedly enhanced certain features. The idea of instincts being "lapsed intelligence" is so clearly and concisely criticized in an article by the late Professor Whitman* that I can not do better than quote an excerpt. His views to the contrary are as follows:

"The view here taken places the primary roots of instinct in the constitutional activities of protoplasm and regards instinct in every stage of its evolution as action depending essentially upon organization. It places instinct before intelligence in order of development, and is thus in accord with the broad facts of the present distribution and relations of instinct and intelligence, instinct becoming more general as we descend the scale, while intelligence emerges to view more and more as we ascend to the higher orders of animal life. It relieves us of the great inconsistencies involved in the theory of instinct as "lapsed intelligence." Instincts are universal among animals, and that can not be said of intelligence. It ill accords with any theory of evolution, or with known facts, to make instinct depend upon intelligence for its origin; for if that were so, we should expect to find the lowest animals free from instinct and possessed of pure intelligence. In the higher forms we should expect to see intelligence lapsing more and more into pure instinct. As a matter of fact, we see nothing of the kind. The lowest forms act by instinct so exclusively that we fail to get decided evidence of intelligence. In higher forms not a single case of intelligence lapsing into instinct is known. In forms that give indubitable evidence of intelligence we do not see conscious reflection crystallizing into instinct, but we do find instinct coming more and more under the sway of intelligence. In the human race instinc-

* Whitman, C. O.: *Animal Behavior, Biological Lectures*, Marine Biological Laboratory, 1898.

tive actions characterize the life of the savage, while they fall more and more into the background in the more intellectual races."

Disease.—Perhaps in the realm of disease more than in any other has an interest in the inheritance of somatic acquirements been manifested. The problem arising here is not essentially different from other questions of inheritance but since it is a matter of such practical importance to man, we may well give it special attention. We have to deal simply with the old questions of what is constitutionally in the germ, what is acquired by the body, and lastly, whether the somatically acquired is inherited. While we all know in a general way what is meant by disease, especially if some specific disorder such as scarlet fever, malaria or tuberculosis is mentioned, an attempt to give an accurate definition is much like trying to define a weed, inasmuch as what is functionally all right at one time or place may be all wrong at another, or what is normal in one animal may be abnormal in another. In general we may say that disease is derangement or failure of physiological function.

Reappearance of a Disorder in Successive Generations Not Necessarily Inheritance.—In attempting to study the inheritance of diseases we must recognize clearly at the outset that reappearance of a disease in successive generations by no means necessarily signifies inheritance. Before it can be pronounced such we must make sure that it is not a case of reimpresing similar modifications on the individuals of successive generations. For example, in England there is a well-recognized condition known as collier's lung which results from constant working in coal mines. And while both father and son may exhibit it, because of their similar occupations, there is nothing hereditary about the malady. Likewise there is what is known as emery grinder's lung, and practically every large manufacturing city with soot-laden atmosphere leaves its impress on the lungs of the inhabitants. This will occur, of course, generation after generation, as long as such pollutions of the atmosphere continue to exist. It is clear that any unhealthy occupation is likely to cause the reappearance of an associated typical disease generation after generation as long as the children follow the calling of their parents. The common misconception that deformities or postures associated with a trade, such as a shoemaker's or tailor's, is genetically stamped on offspring by the end of the

third or fourth generation results from failure to discriminate between real inheritance and mere reappearances under similar conditions of environment.

Prenatal Infection Not Inheritance.—Again, we must recognize that prenatal infection is not inheritance. We have already seen that the young mammal undergoes a certain period of intra-maternal development, but influences operating on it during this period of gestation must be reckoned with as environmental, not germinal. For example, it is said that an unborn child may take smallpox from its mother but this and all similar occurrences are cases of contagion. We find the great pathologist, Virchow, who with many others of his time was a believer in the inheritance of acquired characters, saying nevertheless regarding such instances that, "What operates on the germ after the fusion of the sex-nuclei, modifying the embryo, or even inducing an actual deviation in the development, can not be spoken of as inherited. It belongs to the category of early acquired deviations which are therefore frequently congenital."

Inheritance of a Predisposition Not Inheritance of a Disease.—We must discriminate sharply also between the inheritance of a predisposition and the inheritance of a disease itself.

We often hear the statement made that tuberculosis is inherited and have cited in evidence certain consumptive families or strains. But tuberculosis is a bacterial disease and children of tuberculous parents are never born with the disease except in the rarest of instances. What is really inherited is a constitutional susceptibility to this particular germ.

With some diseases such as leprosy, typhoid fever, smallpox and cholera there seems to be less a question of special susceptibility since nearly all persons are vulnerable. Yet in cases of typhoid, at least, there are some indications that certain families are more likely to take the disease than others under similar exposure. We know of no inherited effects of such diseases, however. For instance, children of lepers do not inherit leprosy and if kept out of leper districts remain normal.

Similar Conditions May Have Different Origins.—In certain abnormal states there is danger of confusing similar conditions which may have two entirely different sources of origin. Deafness, for example, may be strictly inborn as the outcome of a germinal variation or it may result from extraneous influences such as accidents, infective diseases, neglected tonsils and

the like. The former is inheritable, the latter not. In such disorders as gout there is little question but that a tendency to its runs in families. On the other hand it may also be acquired without special susceptibility. There is no evidence, however, that because a father has gout the effect of the gout is reflected on to his germ-cells and the son has gout as a result. Indeed, often a son who becomes gouty was born long before the father became gouty. Son and father both have gout then, because each has innate germinal tendencies which when subjected to certain evocative stimuli become expressed as gout.

Other Disorders Which Have Hereditary Aspects.—Space will not permit discussion of various other specific disorders which are known to have important hereditary aspects, although none shows any convincing evidence of having become hereditary in nature through first affecting the soma. Some of these, such as epilepsy and other nervous affections, tuberculosis, cancer, color-blindness, cataract and various malformations, have already been mentioned. Others that may be listed are arterio-sclerosis, obesity and certain forms of rheumatism, and of heart and kidney diseases. In practically all of these cases in which heredity enters as a factor the condition is one of inheriting a special susceptibility and not the disease itself. Which means simply that the disorder in question is much more easily called forth in such persons by appropriate bacterial or other stimulus, than in the case of the normal individual.

Serological Experiments.—If influences originating in the body can be transmitted to the germ-cell, the most obvious means of conveyance in higher animals is the blood.

Foreign proteins of either plant or animal origin introduced into the blood stream of an animal will cause the formation of certain antagonistic or corrective substances to which the general name of *antibody* is applied. The protein substance employed to produce antibodies is commonly called the *antigen*. Although there are several classes of antibodies—*precipitins*, *agglutinins*, *bacteriolysins*, *cytolysins* or *cytotoxins*, etc.—they all have certain points of similarity, as, for instance, their means of origin, their reaction to heat, and, in some cases, their mode of operation. Chemically their natures are still unknown. Agglutinins, as the name implies, are agglutinating substances. Bacterial agglutinins, for instance, clump bacteria of the species used in their production, if the two are brought together in the

blood-serum of the animal into which the bacteria were originally introduced. Precipitins are substances which form a precipitate when the blood-serum of the treated animal and an extract of the tissue used as antigen are brought together *in vitro*; and cytotoxins or cytolytins are antibodies which possess a toxic, solvent or neutralizing action for the kind of protein used in their production. The various antitoxins in use in medical practise exemplify this latter type of antibody.

In the main the immunologic reactions show a considerable degree of specificity; the antibody will react fully only with the particular kind of protein used as antigen. The specificity is not absolute, however; a milder reaction may be obtained with corresponding proteins of related species, the extent of the reaction being determined by the nearness of the relationship of the species to that from which the original antigen was obtained. With bacteria, the reaction is in the main specific, although so-called group reactions may appear. The serum of an animal immunized against typhoid, for example, may not only agglutinate *Bacillus typhosus*, but may also show this reaction in a less degree with such related forms as the colon bacillus.

Before leaving this subject of specificity, it should be further pointed out that a so-called "species-specificity" and an "organ-specificity" are recognizable in certain serological reactions. By species-specificity is meant the fact, shown through precipitin reactions, that blood immunized against one tissue taken from a given species of animal will react, although in a less degree, with extracts of the other tissues of that species. Thus the blood-serum of a rabbit which has been treated with sheep blood-serum will form a precipitate not only with sheep-serum, but to some extent also with extracts of sheep-muscle, sheep-liver, sheep-spleen, and other organs of the sheep. On the other hand, that there may be organ-specificity also is shown by the fact that immunization with crystalline lens of one species of animal yields a precipitin which reacts with the lens proteins of various other species. Here again, however, the reaction against the kind of lens used as antigen is stronger than against the lens of a different species of animal, so that even in cases of organ-specificity there is still a demonstrable individual specificity. For example, the serum of a goat immunized against pig-lens yields a much heavier precipitate with extract of pig-lens than does this same serum when tested with extract of rabbit-lens.

If it is possible to originate in living animals antibodies which will modify or destroy particular tissue elements the question arises, is it not possible to secure similar selective action on the parts of the developing embryo? Or may there not be sufficient constitutional identity between the elements of the somatic cells and those of the germ-cells that the latter may be specifically modified by such serological influences as can provoke specific changes in tissue elements?

In an attempt to find answers to questions of this kind, the present writer and a research associate, Dr. E. A. Smith, began various experiments with lens antibodies and with *Bacillus typhosis* some years ago, which are still in progress. In the first experiment* the lenses of newly killed young rabbits were pulped thoroughly in a mortar and diluted with normal salt solution. About four cubic centimeters of this emulsion were then injected intravenously or intraperitoneally into each of several fowls. Four or five weekly treatments with such lens-emulsions were given. A week or ten days after the last injection the blood-serum of the fowls was ready for use. The rabbits had been so bred as to have their young advanced to about the tenth day of pregnancy, since from the tenth to the thirteenth day seems to be a particularly important period in the development of the lens; it is then growing rapidly and is surrounded by a rich vascular network that later disappears. From four to seven cubic centimeters of the immunized fowl-serum were injected intravenously into the pregnant rabbits at intervals of two or three days for from ten days to two weeks. A number of the rabbits died from the treatment and many young were killed in utero. Of sixty-one surviving young from mothers thus treated, four had one or both eyes conspicuously defective and five others had eyes that were clearly abnormal. It is possible that still others were more or less affected, as they were judged only by conditions easily visible. In some of the descendants of this stock, indeed, ophthalmologists who have examined the eyes more thoroughly have pointed out defects which the experimenters had overlooked, and occasionally rabbits, that in their earlier months passed for normal, have later manifested defects in the lens or in other parts of the eye.

The commonest abnormality seen in both the original sub-

* Guyer and Smith, *Jour. Exp. Zool.*, Vol. 26, May, 1918; Vol. 31, Aug. 1920.

jects and in their numerous descendants was partial or complete opacity of the lens usually accompanied by reduction in size of the eye. In a few of the later strains in a different experiment, however, several cases of enlargement of the eye, or *buphthalmia*, occurred. Other common defects which have appeared are cleft iris, displacement of the lens, bluish or silvery colors instead of the characteristic pink of the albino eye, microphthalmia, and even almost complete disappearance of the eyeball. The cases of cleft iris, or coloboma, range all the way from a narrow slit in the lower edge of the iris to a broad wedge- or U-shaped opening which amounts practically to the absence of the entire lower part of the iris. The cleft may be confined to the iris or it may extend back deeper into the eye. Of more than one hundred of the eyes which have been carefully mounted and studied by an ophthalmologist, Dr. F. A. Davis, every one showed some degree of coloboma. When one takes into account the embryology of the eye it is not unreasonable to suppose that the defects may all be attributable to initial lens disorder which induced aberrancies or suppressions of normal eye development.

A second defective-eyed line (the so-called 16A1 line) from stock unrelated to the first line (3A1 line) was subsequently established by the use of lens-treated fowl-serum, and still a third unrelated strain (84 line) was secured by directly injecting pulped rabbit-lens intravenously into the pregnant mother thus leading her to develop antibodies in her own blood. Only one of eleven rabbits thus injected produced defective-eyed young.

The experimenters also secured lens defects on two separate occasions in young guinea-pigs by treating one pregnant mother with pulped swine lens, another with pulped rabbit lens—but the young in question died before the inheritability of the condition could be determined. Finally another investigator working in the author's laboratory with pedigreed lines of a large variety of rabbit known as New Zealand Reds, secured one defective-eyed young individual by employing on the mother sheep-serum immunized to rabbit-lens.

As reported in their various papers on the subject the experimenters had many more negative than positive results. It should also be recorded that several investigators who have attempted to repeat the experiments have obtained only negative result with possibly one doubtful exception. The condition is evidently not an easy one to induce. Many complex factors are involved

in such experiments and it is extremely difficult or even impossible to secure similar conditions in all respects. Passing over other differences in technique it may be pointed out that these investigators appear to have used lenses of adult or nearly mature animals as antigen, while in the main Guyer and Smith used the lenses of very young rabbits. Older lenses are tough and are even partially pulped with difficulty, whereas, the lenses of young rabbits go into almost complete solution or suspension. There may have been quantitative or even qualitative differences involved, therefore, in the original antigen.

The fact of greatest interest in the experiments is that once the defect is established it is hereditary. The same genetical conditions hold for all lines. In the 3A1 line, for example, without any further serum treatments it was inherited through nine generations, until that strain was practically exterminated in a series of epidemics which swept through the experimenter's rabbit colony in 1923 and 1924. There is no reason apparent why such defects may not be transmitted indefinitely. The imperfections tended to become worse in successive generations, and also to occur in a proportionately greater number of young. This suggests the possibility that the degenerating eyes might themselves be directly or indirectly originating antibodies or other chemical substances in the blood stream of their bearer which in turn affect the germ-cells. For such bodies once established, should be as effective in modifying germinal factors as corresponding anti-bodies introduced into the fetus through the placenta. Certain it is that an animal will on occasion build antibodies against its own tissues when these are modified, for the writer has repeatedly caused the production of spermatotoxins in rabbits by intravenous injections of their own spermatozoa and the origination of lens precipitins in the blood stream through needling the lens in the eye.

The transmission is not infrequently of an irregular unilateral type (Fig. 84, p. 274), sometimes only the right at others only the left eye showing the defect. In this respect it resembles genetically such anomalies as brachydactyly or polydactyly in man. In later generations there was an increasing number of young with both eyes affected. The abnormal condition has in general the characteristics of a Mendelian recessive. When either defective-eyed males or females are bred to normal-eyed individuals from other strains, for instance, with rare exceptions,

only normal-eyed progeny result in the first generation, but the abnormal condition may be made to reappear in subsequent generations if appropriate matings are made. Two defective-eyed rabbits bred together, however, are likely to produce some normal-eyed young—a fact which indicates that we are not dealing with a simple Mendelian recessive. Probably more than one pair of unit factors are involved.

That the transmission of the defect from generation to generation is not merely the passing on of antibodies by way of the placenta from mother to young, is assured by the fact that

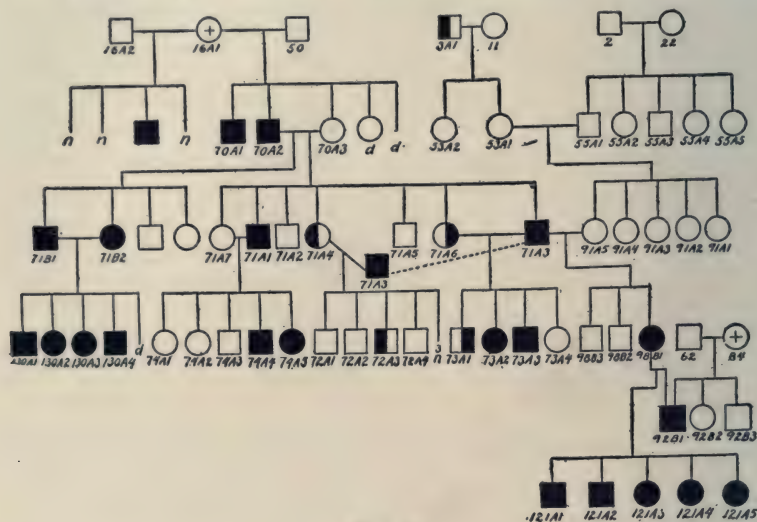


FIG. 84

Chart showing pedigree of some of the defective-eyed rabbits. Only a few of the numerous matings are shown. The circle with the + sign in it indicates the female treated with lens-immunized fowl-serum (16A1) or directly with pulped rabbit-lens (84). The mother of 3A1 was treated with lens-immunized fowl-serum. Squares indicate males; circles, females; symbol all black, both eyes defective; right half black, right eye defective; left half black, left eye defective; unshaded, presumably normal-eyed; d, died; n, normal. Males 16A2, 50 and 2 (upper row) were of normal untreated stock, as were females 11 and 22. Male 62 (fourth row) was of normal untreated stock, while female 84 was injected directly with pulped lens.

descent has been repeatedly established through male lines. Females from strains of rabbits unrelated to the treated stock when mated to defective-eyed males bear normal-eyed young,

but when such young are mated to defective-eyed males or to males of their own derivation, the defect reappears in some of the progeny, after the manner of a Mendelian recessive. It is plain that the abnormal condition could have been introduced into these new strains only through the germ-cells of the defective-eyed males, and its transmission is, therefore, an example of true inheritance. Fig. 85, p. 276, for example, is a chart representing breedings, through which the defect introduced through male 3A1 was made to reappear in his great grandchildren after it had passed in a recessive condition through two normal-eyed females in one generation and a normal-eyed male and a normal-eyed female in the next generation.

The first suggestion that occurs to a geneticist when he encounters such an experiment is that perhaps by inbreeding the experimenters have merely uncovered a recessive defect already present in the stock. In reply to this as regards the first defective (3A1) line it can be said that other litters from the same parents were secured and none of them nor their numerous descendants, although bred as brother and sister matings, have shown the defects. Even when 3A1, the first defective-eyed male secured, was bred back to his mother, the five resulting young had normal eyes. Likewise, in the second line, intensive inbreeding was practised among the untreated brothers and sisters of 16A1 and their progeny and none but normal-eyed offspring was secured. But even supposing the experimenters by chance just happened in their first experiment to hit upon an individual which was carrying a recessive eye defect ready to be revealed in her descendants after treatment with serum immunized against rabbit lens, it is improbable that a similar defect would also happen by chance in the unrelated 16A1 line, and the theory of chance surely becomes untenable for a third (84) line, to say nothing of the case secured in a pedigreed line of New Zealand Reds or the two cases mentioned in guinea-pigs. Whatever the final explanation of just what has taken place in the germ-plasm may be, it seems reasonably sure that the results are in some way the outcome of the experimental treatment.

While it is true that animals with congenitally defective eyes do appear occasionally in such animals as rats, mice, guinea-pigs and rabbits, such anomalies are certainly by no means common in rabbits. In more than two thousand young born during the writer's work with rabbits he has encountered only one instance:

an apparently normal female produced one totally eyeless and one abnormally small-eyed young in the same litter. Even such so-called "spontaneous" defects, however, do not arise uncaused though we are ignorant of the cause.

The question of whether the effect is a general one due to a general poisonous or inhibitive influence or whether it is a specific one due directly to lens-antibodies in the blood-serum is a difficult one to answer certainly. The general inclination of an embryologist, knowing how susceptible in early embryogeny

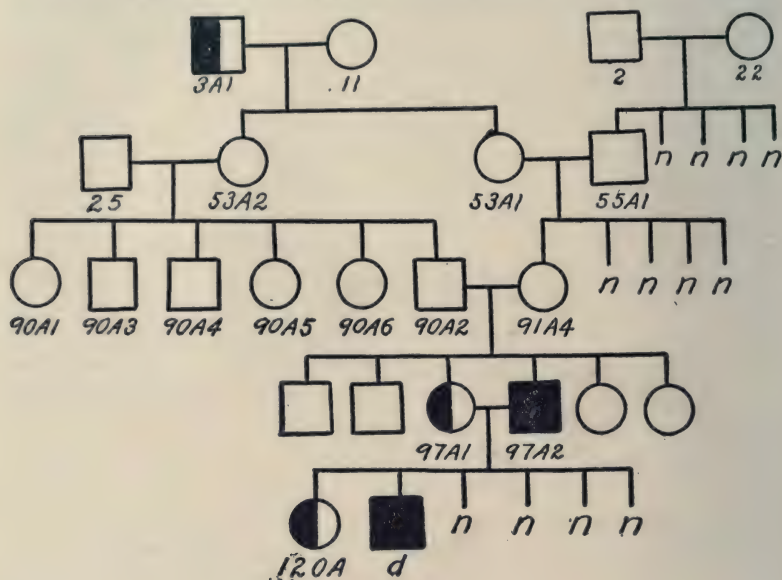


FIG. 85

Inheritance of the defects through the male line. Symbols same as in Fig. 84. Individuals 11, 2 and 22 were of normal, untreated stock, hence the defects seen in the 97A and 120A series could only have been derived from the albino male, 3A1. Pigmentation was introduced into the stock through male 25. The defective-eyed 97A1 and 97A2 are pigmented.

the eye is to any kind of deleterious agent, is to regard the result as of the general type exemplified in the chapter on the mechanic of development (Chap. V). The evidence from the experimenters' controls, however, all points toward specificity. Never in well over fourteen hundred young born from mothers which had been subjected to just as violent or even more violent sero-

logical treatments in various other experiments has a single instance of eye defect appeared. Eye abnormalities have occurred only when a foreign serum which contained lens antibodies was used, or when the mother's own serum carried antibodies developed against lens injected directly or against her own lenses, following injury, after the manner to be next described.

In later experiments the writer found that, when its lens is injured, a normal rabbit will frequently develop lens antibodies in its own blood-serum. In such operations the eye is treated with a local anesthetic, then pierced with a needle by means of which the lens is more or less broken up. The procedure is the same as that commonly followed by ophthalmologists in cases of children with congenital cataract. The serum of all rabbits used in such experiments was first tested for rabbit-lens precipitins and without exception found negative. In from 7 to 10 days after the needling operation the serum of each rabbit was again tested for lens precipitins. Of 23 rabbits thus treated, 10 gave negative, 2 questionable, and 11 positive results. Some of those which were negative after the first operation gave positive reactions after a second operation.

A number of rabbits are under experiment at present to determine whether or not transmitted defects similar to those of the earlier experiments result from this method. These experiments are of too short duration to be reported in detail beyond relating that out of 33 needled females (some of them reneedled between litters) five have borne one or more young in some of their litters with one or both eyes defective. The most interesting case is that of defective young obtained from a normal female with uninjured eyes bred to a needled-eyed male. The first litter of three died before their eyes could be examined; the second litter of four contained three with defective eyes; and the third litter of three had one defective-eyed individual. If this experiment can be repeated it becomes the most significant of all since the defect must have come from the injured male and not from the normal female. It thus eliminates the equivocal condition which always exists because of the placental relations when the female is the source of the defect.

Whether or not the eye defects induced thus by direct operation on the parents are inheritable remains yet to be determined. Most of the young secured in these last experiments died in an epidemic which swept through the stock of experimental animals. The experiments, however, are being continued.

In a later experiment with albino rats the writer obtained 308 normal-eyed young from 20 needled-eyed mothers. That is, there was no perceptible effect on any of the young. On the other hand, when 68 female and 5 male guinea-pigs were similarly needled and mated, 60 of the females bore 92 young, among which were 11 defective-eyed young from 8 different mothers. These two sets of results raise the question of whether or not certain kinds of animals may not be more susceptible to such operative procedure than others. Also it suggests the possibility that certain strains of the same kind of animal may be more easily influenced by such operations than others. This matter is being investigated at present.

Do the results of the earlier experiments afford an example of the inheritance of a somatic acquirement? The experimenters have never maintained that they do. They are suggestive, so far, rather than conclusive. The truly hereditary nature of the anomaly is beyond question and there is little reason to doubt that it has been engendered in some way by means of the serum treatments. One's inclination from knowledge of the field of experimental embryology is to attribute the initial defect to a general poisonous or inhibitive agent, yet all the results in the actual experiments checked by our fourteen hundred controls, point to it as specific rather than general. Never was the defect obtained except in association with a serum carrying specific antibody.

It is not yet clear whether the eye of the fetus is first changed and the condition is then conveyed from it to the germ-cells of this individual, or whether the eye and the germ of the fetus are influenced separately by the antibodies which have entered from the mother's blood by way of the placenta. Only the first occurrence could be interpreted as the inheritance of a somatic change; the second would be an instance of what is known as *parallel induction*. Strictly interpreted, even in the defective-eyed young of mothers with needled lenses, provided the condition proves inheritable, the same two alternatives confront us. Until adequate outbreeding experiments with needled-eyed males have been made the question must remain unanswered. Such experiments are in progress.

CHAPTER XVII

PRENATAL INFLUENCES

All That a Child Possesses at Birth Not Necessarily Hereditary.—We come now to the more specific discussion of what may happen to offspring of mammals, and particularly man, in the interval between fertilization and birth; that is, during the intramaternal period. We have already seen that anything affecting the offspring during this period has to be reckoned as environmental, our formula reading, Mammal = germ + intra-maternal environment + external environment. It is evident, then, that all that a child possesses at birth is not necessarily hereditary, since the unborn child may be influenced by conditions prevailing in either parent.

The Myth of Maternal Impressions.—In order to clear the way for more urgent matters let us first inquire into the question of the production of changes in the unborn child as a result of "maternal impressions." As the tale generally goes, structural changes are produced in the unborn child corresponding to some mental experience of the mother, usually a vivid impression or strong emotion, but when a given individual is pinned down to sources, it is usually a case of hearsay.

Stock examples are: The mother sees a mouse with the result that a mouse-shaped birthmark occurs on the child; or she sees a crushed hand and in consequence bears a child later with some of the bones of the hand missing; the mother touches her body when frightened and thus marks the unborn child on the corresponding part of the body; or she produces beauty in the child by long contemplation of a picture of a beautiful child; and so on almost endlessly. The favorite is usually the production of a red birthmark or marks on the child's body by strong desire on the part of the mother for strawberries, tomatoes, etc.—the fruit must be red since the mark is red—or by fright from seeing a fire. As a matter of fact it is not uncommon for the small blood-vessels of the skin of a new-born infant to remain dilated in spots instead of contracting as they normally should

do. The result is more or less of a red or "flame" spot. It is easy to see, therefore, why such birthmarks are so frequently referred back by the credulous mother to her desire for or fear of some red object.

An analysis of the case of a child shuddering at the sight of peaches is of interest in this connection. The child showed the greatest aversion to peaches, particularly to the fuzzy covering. The mother's explanation was that peaches were unusually plentiful the year the child was born and that she had worked hour after hour at peeling and canning peaches shortly before his birth until she had become thoroughly sick of them. This acquired aversion on her part she believed had been transferred to the child. A few questions revealed the fact, however, that the mother, herself, had never liked peaches and when asked if they were distasteful to any other member of her own family she exclaimed, "Oh, yes, my mother would shudder and shake if a peach were brought near her." And there we have it. The idiosyncrasy was an inherited one as many similar peculiarities are. The mental impression produced in the mother by her own experience with peaches had nothing to do with its occurrence in the child.

Frequently also one encounters the mother who is sure she has engendered musical ability in her child by constant practise and study of music during pregnancy. The child is musical; what better evidence does one want! It seems never to occur to such a mother that the child is musically inclined because she herself is, as is evinced by her own desire in the matter even if she is not a skilful performer.

The following wholly unwarranted statement is a sample of the misinformation and nonsense which characterize most books on so-called "Maternal Impressions" or "Prenatal Culture": "It is admitted that the mother can and does destroy and build up nerve cells by the action of her mind, as in the case of simple birthmarks. It can not be successfully controverted that a mother does add flesh, bone and sinews in the case of monstrosities—takes from one part and adds to another——." Concerning the multitudes of cases where the conditions are such that, on the theory of maternal impressions, something *should* happen, but nothing does, the book just quoted vouchsafes a naive explanation in the following example:

"Mrs. B. of R——, a short time after her marriage, was sitting alone sewing, when a tramp came to the door, put both arms against the screen door and in a rough voice said, 'Can't you give me something, I ain't got no hands?' Mrs. B. put both hands up to her face and screamed, 'Mother! Mother!' The mother drove the tramp out of her sight, but Mrs. B. could not get him out of her mind, and continually wished and hoped that her child would have perfect hands. That was her continual prayer up to the time of its birth; the child was born with perfectly formed hands; in fact, no defect of any kind was noticeable. She is at this writing 14 years of age. This scare may have done some injury to the forming brain or body, as it was a severe shock to Mrs. B., and we have a right to assume that it arrested the development; but her longing and praying, 'Oh, I hope that my child will not be injured by this shock which I have experienced,' is the reason why it was not affected, and accounts for the facts, etc.—"

It is unnecessary to point out that a "science" built upon such a "heads I win, tails you lose" system as this would not have to go far afield to produce "proof" of almost any claim.

Practically all the organs of the embryo are well established by the end of the second, or certainly by the end of the third month, often before the mother is sure she is carrying a child, yet marked alterations are supposed to occur from something which is thought or which happens late in pregnancy! If a finger or a toe or a hand could be caused to be missing by the sight of an accident, we should have to suppose that it had been destroyed in the fetus after having once been formed.

When we take into account the extreme credulity of many people, the unconscious tendency of mankind to give a dramatic interpretation to events where causes are not certainly known, the hosts of coincidences that occur in life, and the multitude of cases where something should happen but nothing does, we are compelled to believe that the whole matter of direct specific influence of the mother's mind on the developing fetus is a myth. After seeing the conditions which prevail in Mendelism, for example, it will take strong faith indeed to believe that a mother with duplex brown eyes can "think" or "will" blue eyes on to her baby, yet this would be a mild procedure compared to some we are asked to accept by believers in the transmission of maternal impressions. Most of all, however, when we recall the actual

relation between the embryo and the mother—a narrow umbilical cord is the sole means of communication between the two—the physical impossibility of a connection between some particular mental happening of the mother and a corresponding specific modification in the fetus becomes evident. For there are no nerves in the umbilical cord, the only path of communication between mother and fetus being the indirect one by way of the blood stream. Even this method of communication is limited inasmuch as the mother's blood does not circulate through the blood-vessels of the fetus. Gaseous and dissolved substances are merely interchanged through the thin walls of the capillary blood-vessels in the placenta.

No Short Cut to Race Betterment.—So far as scientific investigations have been able to penetrate the matter, the beneficial results of conscious endeavors on the part of mothers to train directly their unborn children are mythical. Just this much there is in it—self-control and cheerfulness on the part of the expectant mother conduces to her peace of mind and consequently favors the normal functioning of her own nutritive and other physical processes. Worry, rebellion, hatred, or other disturbances of mental tranquillity may in a general way react unfavorably on the unborn child provided the disturbance is of sufficient magnitude to interfere with the normal functions of the mother, but it must do so through the nutritive channels which supply the unborn young. In other words, while conceivably it is possible to influence the fetus adversely there is no known mechanism by which it can be influenced favorably beyond that furnished by a wholesome unpoisoned nutritive supply in the blood stream of the mother.

Injurious Prenatal Influences.—However, the denial that a particular mental impression of the mother is associated with a particular structural defect in a child does not carry with it the implication that prenatal influences of all kinds are negligible factors. On the contrary any deleterious effect which can reach the fetus through absorption from the blood of the mother may be of grave consequence. There is not the least doubt that malnutrition or serious ill-health on the part of the mother often has a prejudicial effect on the unborn offspring. It is estimated, for example, that in seventy-five per cent. of women who have typhoid fever during pregnancy the fetus is aborted or stillborn. Severe shock or grief, worry, nervous exhaustion,

the influence of certain diseases, poisons in the blood or tissues of the parent, such as lead, mercury, phosphorus, alcohol and the like, may all act detrimentally, but they operate either by rendering nutrition defective, by direct poisoning, or by generating toxins in the blood of the parent which then poison the fetus. Among the latter may be mentioned the toxic products of tuberculosis and certain other bacterial diseases. Such factors operating on the unborn young or possibly even on the germ-cells may cause malformations, arrests of development, instabilities of the nervous system, and general physical or mental weakness. The effects are general, however, and not specific.

To distinguish certain of these prenatal effects, particularly those of certain diseases or poisons, from true hereditary influences they are frequently spoken of as cases of *transmission* rather than inheritance from parents. The technical term *blastophthoria*, is used to designate damage that is inflicted directly on the germ-cells.

Lead Poisoning.—By way of illustration of how certain cumulative poisons may act we may examine a tabulation of eighty-one cases of lead poisoning as reported by Constantin Paul (Fig. 86, p. 284).

The table requires little comment. The disastrous effects of such poisoning are apparent in every class of cases. The sixth class where the husband alone was exposed to lead shows that the poison can operate directly through the germ-cell. Other observers note that in the children of workers in lead, there is a distressing frequency of feeble-mindedness and epilepsy.

That lead poisoning operating through the germ-cells of the father can affect the development of the young harmfully is well shown in Fig. 87, facing p. 284, which is a photograph of two young rabbits from the same litter. The white young one is from a normal albino mother mated to an albino father which had received lead treatment. The pigmented young one is from the same albino mother by a normal pigmented father. Although the white father was considerably larger than the pigmented father, nevertheless the young of the former, because of the harmful effects of the lead, is distinctly smaller and less lively. A number of litters, each from the same mother but in part from a lead-poisoned father and in part from a normal father, were secured by Professor Cole. All showed more or less the same results.

The Expectant Mother Should Have Rest.—The mere matter of rest on the part of the pregnant mother is, judging from the work of Pinard, a Frenchman, and his pupils, an important one. In a number of detailed investigations they have shown that rest on the part of the working mother during the last three months before the child is born results in the production

	Number of cases.	Number of pregnancies.	Abortions, premature labor, and stillbirths.	Infants born living.	Remarks.
1. Mother showing symptoms of plumbism.....	4	15	13	2	One infant died within twenty-four hours.
2. Mother working in type foundry, all of whose previous pregnancies had been normal.....	5	36	29	7	Four of these died in first year.
3. Mother who during period of work in type foundry had five pregnancies	1	5	5	0	After ceasing to work had healthy child.
4. Mother working intermittently in type foundry; while working there	3	3	3	0	When away from work for some length of time gave birth to healthy children.
5. Mother in whom blue line of gum the only sign of lead poisoning..	6	29	21	8	
6. Husband alone exposed to lead	?	32	12	20	Of these, eight died in first year, four in second, five in third.

FIG. 86

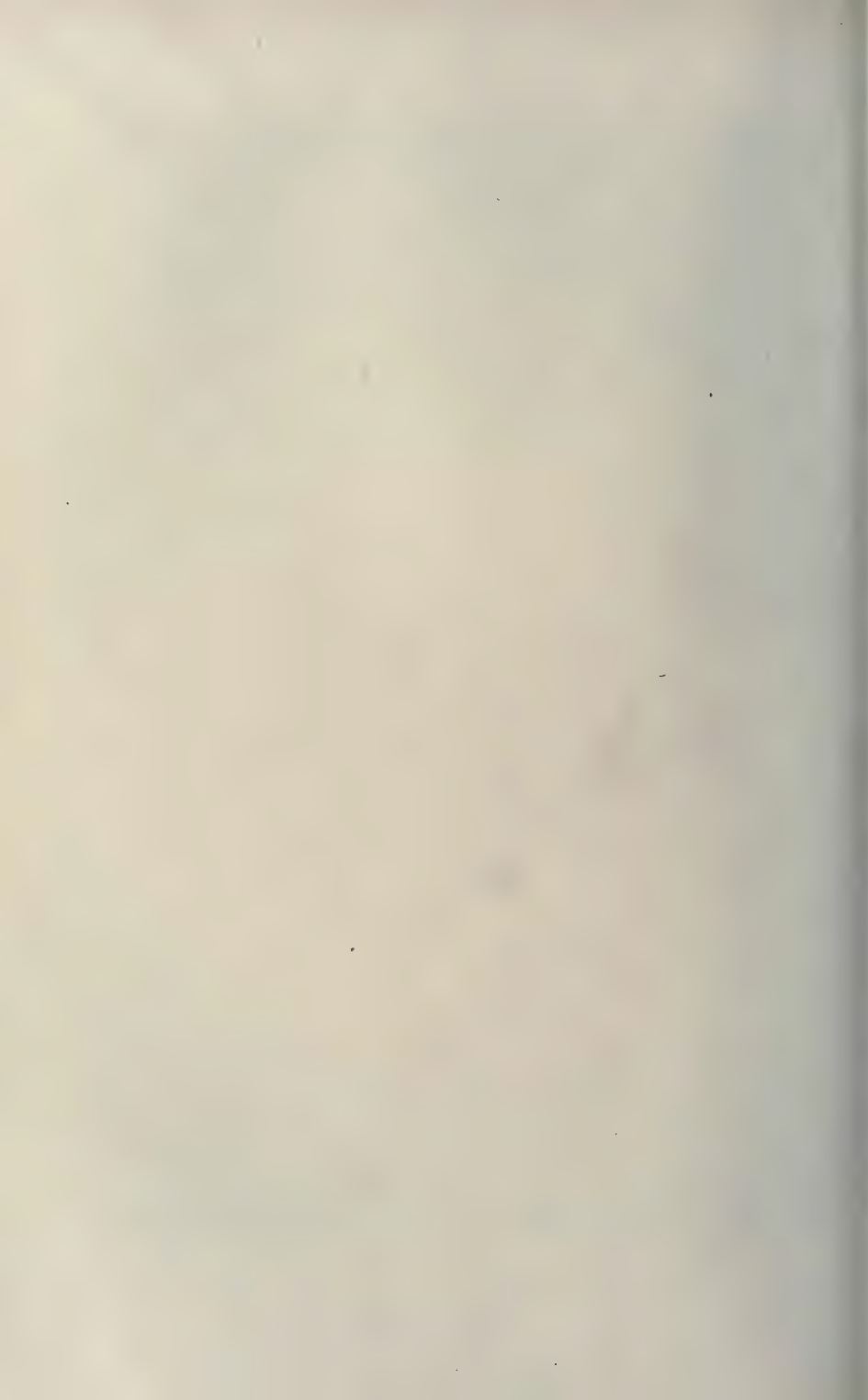
Tabulation of eighty-one cases of lead poisoning recorded by Constantin Paul (from Adami).

of markedly larger and more robust children than those born of mothers equally healthy but who have not had such rest. Moreover the danger of premature birth is considerably lessened.

Too Short Intervals between Children.—Too short an interval between childbirths would also seem to be an infringement on the rights of the child as well as of the mother. Thus Doctor R. J. Ewart ("The Influence of Parental Age on Offspring," *Eugenic Review*, October, 1911) finds that children born at intervals of less than two years after the birth of the previous



FIG. 87. Photograph of young rabbits from the same litter, the smaller one stunted by lead poisoning of its father.
(Courtesy of Professor L. J. Cole.)



child still show at the age of six a notable deficiency in height, weight and intelligence, when compared with the children born after a longer interval, or even with first-born children.

Our Duty to Safeguard Motherhood.—Doubtless the unventilated factory and tenement also do their share, even though we can give no exact quantitative measure of it. Obviously, it becomes a civic duty to protect as much as possible all members of our social system from such injurious factors as have just been discussed. It is particularly necessary to safeguard mothers before confinement, especially working mothers.

Expectant Mothers Neglected.—According to the claims of life insurance men, expectant mothers are the most neglected members of our population. Doctor Van Ingen, of New York City, estimates that ninety per cent. of women in this country are wholly without prenatal care. Yet every prospective mother should be taught the probable meaning of such symptoms as headaches, hemorrhages, swelling of the feet and disturbed vision. She should realize the importance of submitting a sample of urine for analysis at least once a month before childbirth and twice a month for a while thereafter. She should be specially informed regarding work, exercise, diet and dress. A government bulletin written by Mrs. Max West which may be had free by writing to the Childrens' Bureau, Department of Labor, Washington, D. C., gives much useful information on this subject.

Transmission of Induced Immunity.—It is well known that after recovery from an attack of any one of certain diseases various animals, including man, are more or less immune to further attacks of the same disease. Immunity may be artificially induced, moreover, by means of antitoxins against such diseases as typhoid fever and diphtheria. The question arises as to whether such immunity is transmitted to offspring. Repeated experiments on guinea-pigs, rabbits and human beings have shown that in such forms the young born of mothers immunized during pregnancy are immune at birth but that the immunity is apparently soon lost. The effect is probably one of direct placental transference from the blood of the mother. Temporary immunity can be produced in young animals indeed by merely having them nurse from an immunized mother. However, Guyer and Smith, using typhoid agglutination tests, found that in rabbits, while the young of normal untreated mothers nursed by immunized mothers lost their acquired titer rapidly

after weaning time, the young born of immunized mothers, even when nursed by non-immunized mothers with negative agglutination titers, maintained their typhoid titer for some months and in some instances even transmitted it to their own offspring. This indicates that in the latter, which have acquired their immunity reactions through placental transmission, some mechanism concerned with the production of antibodies has been influenced in the young which was left untouched by such passive transfers as occur through milk. Moreover, Guyer and Smith found that in subjecting successive generations of rabbits to typhoid inoculations, considerably higher agglutination titers (and presumably therefore increased immunity to typhoid) could be developed in individuals of strains which had been under immunization for three or four generations than in first generation animals or in previously untreated stock. Whether subsequent experimentation shows this to be a truly hereditary immunity or merely a cumulative placental transmission, the practical possibility presents itself that by such means a general population might in time be made to become more or less immune to a disease.

ALCOHOLISM

Unreliability of Much of the Data.—One of the most important poisons that may play a prominent part among antenatal influences is alcohol. But when it comes to a study of the problem of alcoholism from the standpoint of heredity and parental influences we meet with many difficulties, prominent among which are the inaccuracy and unreliability of many of the statistics brought forward in this connection. Many of the results are vitiated by the prejudices of propagandists who propose to make a case either for or against alcohol as a beverage whether or not the facts justify their conclusions. When one tries to view the matter with an open mind he finds that there is a deplorable lack of statistics which are not susceptible to more than one interpretation. However, using as much as possible what seems to be unbiased data, the evidence is almost wholly against alcohol as a beverage, at least to any immoderate extent.

Alcohol as a Germinal or Fetal Poison.—The bad effects as far as offspring are concerned reveal themselves in the main

under the category of "false heredity," i. e., germinal or fetal poisonings rather than of heritable changes induced in the germ-cells. Most investigators feel that there are too many criminal, imbecile, insane and unhealthy persons among the offspring of drunkards to dismiss the matter as a coincidence. In an investigation of Imbault, for example, we find recorded of one hundred tuberculous children that while forty-one were of tuberculous parentage, thirty-six per cent. were the offspring of inebriates. Furthermore Imbault cites the observations of Arrivé on 1,506 cases of juvenile meningitis to the effect that this malady is twice as frequent in the children of alcoholic as in those of tuberculous parentage. It has been proved by Nocloux (*L'Obstétrique*, Vol. 99, 1900) that in dogs and guinea-pigs alcohol passes through the placenta and may be detected in fetal tissues; hence it is in position to influence the fetus.

There is evidence, however, that mature sperm-cells may show considerable resistance to alcohol. Thus Ivanow has shown that spermatozoa of the rat, rabbit, guinea-pig, sheep and dog can be treated with alcohol up to a strength of seven per cent. and yet produce vigorous normal progeny when females were artificially impregnated with them. Gee found that the spermatozoa of fishes require almost a lethal dose of alcohol before they become so injured that they cause abnormal development in eggs they fertilize.

Progressive Increase in Death-Rate of Offspring of Inebriate Women.—In an investigation on the effects of parental alcoholism on the offspring, Sullivan (*Journal of Mental Science*, Vol. 45, 1899) gives some important figures. To avoid other complications he chose female drunkards in whom no other degenerative features were evident. He found that among these the percentage of abortions, stillbirths and deaths of infants before their third year was 55.8 per cent. as against 23.9 per cent. in sober mothers. In answer to the objection that this high percentage may be due merely to neglect, and not to impairment of the fetus by alcoholism, he points out the fact based on the history of the successive births, that there was a progressive increase in the death-rate of offspring in proportion to the length of time the mother had been an inebriate, thus:

	No. of cases	Per cent. born dead	Per cent. dying before 3	Total percentage
First births	80	6.2	27.5	33.7
Second births.....	80	11.2	40.8	52.0
Third births	80	7.6	45.0	52.6
Fourth and fifth	111	10.8	54.9	65.7
Sixth to tenth	93	17.2	54.8	72.0

Views of a Psychiatrist on Alcohol.—Forel, who for years was the psychiatrist at the head of a large insane asylum at Zurich, Switzerland, has this to say about the effects of narcotic poisons and alcohol in particular:

“The offspring tainted with alcoholic blastophthoria suffer various bodily and physical anomalies, among which are dwarfism, rickets, a predisposition to tuberculosis and epilepsy, moral idiocy, and idiocy in general, a predisposition to crime and mental diseases, sexual perversions, loss of suckling in women, and many other misfortunes.”

Other Views.—Many competent investigators, on the other hand, believe that alcoholism in parents has little or no part in the direct production of mental defects in children. For instance, Tredgold quotes Doctor Ireland's observations that although at New Year, when the fishermen return, the whole population of certain villages in Scotland gets drunk, there is no noticeable excess of defectives born nine months later, and remarks further that, “I have histories of idiots conceived under such circumstances, but so I have of normal children, and my opinion is, that while this may be a cause in some cases, the number of instances in this country at any rate is exceedingly small.” Again, Goddard, one of our best-known American students of feeble-mindedness, who has made careful study of this point under especially favorable conditions, feels that his data do not prove that alcoholism of either the father or the mother causes feeble-mindedness in the child. He concludes, “Everything seems to indicate that alcoholism itself is only a symptom; that it for the most part occurs in families where there is some form of neurotic taint, especially feeble-mindedness.” Goddard, however, in common with many other observers, notes that miscarriages and deaths in infancy are far higher among inebriates than among abstainers.

Doctor Mjöen cites an interesting parallel between the increase of feeble-mindedness in Norway and a period from 1816 to 1835,

when every one was permitted to distil brandy. In some districts many of the farmers distilled brandy from corn and potatoes, and in such regions during this period feeble-mindedness increased nearly one hundred per cent. Later the home distillation of brandy was stopped. According to Doctor Mjöen, "The enormous increase in idiots came and went with the brandy." He is inclined to believe, however, that the alcohol operated injuriously mainly on stocks already defective.

Innate Degeneracy Versus the Effects of Alcohol.—Many observations on human beings have been brought forward which at first sight seem to indicate that noticeable defects, particularly mental and nervous, occur with appalling frequency in children resulting from conception during intoxication, although, unfortunately, the evidence is rarely clear as to whether the defects are really due to the effects of the alcohol or to the fact that the parent or parents were degenerate to begin with.

A very interesting human case cited by Forel on the authority of Schweighofer is that of a normal woman who had three sound children when married to a normal man. After the death of this husband she married an inebriate by whom she had three other children. One of these suffered from infantilism, one turned out to be a drunkard, and the third became a social degenerate and drunkard. Moreover the first two contracted tuberculosis, although hitherto the family stock had been free from this malady. Ultimately the woman married again and by this third husband, who was normal, she again had sound children. Similar cases might be cited, as, for example, a record of eighty-three epileptics, of whom sixty had drunken parents, but it can be urged against all of them, of course, that the defective offspring were due to an innate degeneracy of the drunken parent which made him a drunkard rather than to the effects of the alcohol he took. While one is skeptical as to the validity of this objection in all of the many cases which occur with such monotonous frequency in man, there is no way of escaping such an interpretation with the evidence at hand. It must be admitted, moreover, that there are many families with one or both parents alcoholic in which the children are not mentally defective.

Experimental Alcoholism in Lower Animals.—Many of the objections that exist in the case of man, however, do not apply in that of lower animals. If normal animals are experimentally

alcoholized and are shown to produce defective offspring under such conditions, then in their cases at least, the disorders in the offspring must be due to the effects of alcohol and not to an innately degenerate condition of the parent. Disorders similar to some of those seen in the children of alcoholics do actually result in alcoholized animals of one kind or another.

Laitinen alcoholized rabbits and guinea-pigs. He found that the treated individuals had more stillborn young than the control, and also that growth of the living young was retarded. His alcoholized rabbits and guinea-pigs produced more young than did the normal individuals used as a control. Laitinen's studies on man, together with three other studies of the Eugenics Laboratory in London, show that in man also more children are born to alcoholics than to normal parents. Goddard's investigations in American corroborate this fact.

Hodge made a pair of dogs alcoholic. Of 23 pups obtained from the pair, 8 were deformed and 9 were dead; 4 alone were viable. From a control pair of dogs 45 pups were obtained, of which 4 were deformed, none were born dead, and 41 were viable.

Against the earlier experiments on animals it has been urged that too few individuals were used to give conclusive results, or that the test animals were not known to be of normal ancestry, but this objection can not be brought against the experiments on guinea-pigs by Stockard in collaboration with Craig and Papanicolaou.

Stockard's Experiments on Guinea-Pigs.—The experiments of Stockard and his coworkers demonstrate that the offspring of mammals may be injured or modified in their development by treating either parent repeatedly with alcohol. The guinea-pigs used in the experiment were all first tested by normal matings and found to yield normal offspring. The alcohol was given to them by inhalation. It was found to be readily taken into the animals' blood and to produce intoxication. While guinea-pigs alcoholized in this way as often as six times a week for two and one-half years would maintain their own bodily vigor and health apparently, the deleterious effects on their progeny were marked. The defects were general rather than specific, although the central nervous system and special sense organs were apparently affected most. Spasms, epileptic-like seizures and eye defects were among the disorders observed. An outstanding fact was the number of sterile matings and of stillborn or short-lived young that occurred.

CONDITION OF THE OFFSPRING FROM GUINEA-PIGS TREATED WITH ALCOHOL

Condition of the Animals.	Number of							Total dead.	Surviving young.
	matings.	Negative result or early abortion.	Stillborn litters.	Number of still-born young.	Living litters.	Young dying soon after birth.			
Alcoholic by normal	90	37	10	20	43	35	55	47	
Normal by alcoholic	33	7	4	12	22	23	35	21	
Alcoholic by alcoholic	41	20	4	8	17	12	20	14	
Summary	164	64	18	40	82	70	110	82	
Control normal by normal	90	22	2	8	66	19	27	99	
Treated during pregnancy	4	0	0	0	4	1	1	7	
Second generation by normal	46	10	3	8	33	29	37	25	
Second generation by alcoholic	53	16	8	17	29	22	38	28	
Second generation by second generation	95	29	7	16	59	43	59	52	
Third generation by third generation	48	20	7	14	21	19	33	13	
Third generation by second generation	33	15	4	8	14	16	24	7	
Third generation by normal	17	3	4	8	10	5	13	7	
Third generation by alcoholic	3	1	0	0	2	2	2	1	
Second, third generation by second, third generation	18	9	2	6	7	6	12	4	

Fig. 88.

Table showing condition of the offspring from guinea-pigs treated with alcohol (after Stockard).

The results are summarized to 1916 in the accompanying table (Fig. 88, p. 291). Later data obtained in part from animals unrelated to those used previously confirm the earlier findings.

Stockard's Interpretation.—Stockard's interpretation of his experiment is as follows: "Mammals treated with injurious substances, such as alcohol, ether, lead, etc., suffer from the treatments by having the tissues of their bodies injured. When the reproductive glands and germ-cells become injured in this way they give rise to offspring showing weak and degenerative conditions of a general nature, and every cell of these offspring having been derived from the injured egg or sperm-cell are necessarily similarly injured and can only give rise to other injured cells and thus the next generation of offspring are equally weak and injured and so on. The only hope for such a line of individuals is that it can be crossed by normal stock, in which case the vigor of the normal germ-cell in the combination may counteract, or at any rate reduce, the extent of injury in the body cells of the resulting animal."

He also believes that various deformities and developmental arrests such as harelip and cleft palate may similarly be cases of transmission rather than true inheritance, due to the weakening of the germ-cells in some way, or to some lack of full vigor in the uterine environment.

Stockard and Papanicolaou found that after the fourth filial generation from the alcoholized forebears the ill effects disappear. Such descendants, in fact, live longer and are more vigorous than the controls. The experimenters believe that, as was maintained by Pearl in an earlier study, this racially beneficial effect of alcohol is due to the elimination of weak germ-cells, defective embryos and poorly developed individuals, or in other words, to the survival of only the strongest.

Pearl's Experiments on Fowls.—Pearl found that the offspring of alcoholized fowls are on the whole superior to those from normal individuals. Abnormal offspring were no more frequent than from untreated fowls, the mean egg production of the treated and the untreated groups was practically the same, but the offspring of the alcoholized fowls developed a higher body-weight than those of the normals. Moreover the death-rate at all ages after hatching was actually lower among offspring both parents of which had been alcoholized. The proportion of fertile eggs, however, was materially reduced when one or both

parents had been treated with alcohol and since this indicates elimination of the weaker germ-cells or early embryos, Pearl does not consider his results as necessarily opposed to Stockard's. The harmful effect of the alcohol apparently permitted the survival of only the most vigorous offspring.

In addition to the foregoing, a further considerable amount of careful research on the racial effects of alcohol on various animals has been done during the past few years: on the fowl (Danforth); on the rat (Hanson, MacDowell); on the mouse (Nice, Bluhm); and on the frog (Bilski). All agree with Pearl in finding that alcohol acts as more or less of a selective agent, both upon germ-cells and developing embryos, eliminating the weak and leaving the strong. The guinea pig is apparently the only type in which defective offspring were produced in early generations by alcoholization, although MacDowell believed that the offspring of his alcoholized rats showed slight reduction in activity and in ability to find their way through a maze. The diminution in fertility which sometimes occurred in earlier generations was usually compensated for by increased fertility in later generations in which presumably only the more vigorous strains were left. What application of these experiments, if any, can be made to man is problematical.

Further Remarks on the Situation in Man.—Returning now to the question of alcoholism in man, it seems in view of the strong circumstantial evidence in the case of man himself, together with the result of experiments on animals, that little doubt remains that excessive alcoholism might result in the production of defective offspring. On the other hand an antecedent degeneracy or neural instability undoubtedly plays an important part in many cases, in the original production of drunkards, and when such occurs, it, as well as the direct effects of alcoholic poisoning, must be reckoned with in the effects on progeny. Studies carried on by Pearson, Elderton and Barrington of the Eugenic Laboratory in London lead these investigators to the conclusion that extreme alcoholism is a *result* not a *cause* of degeneracy. That is, the degeneracy is due to the defective stock, not to alcohol. They cite in evidence their records of four thousand school children of alcoholic and of sober parents, which fail to show any unfavorable effect of alcohol on offspring. Some of their critics, however, maintain that they did not choose subjects who were sufficiently alcoholic to give the injurious

results that might legitimately be expected among the offspring of excessive drinkers or habitual drunkards.

Where children show a hereditary inclination toward drink, unquestionably one of the strongest factors is the inheritance of the same disposition, the same unstable nervous constitution and its accompanying lack of self-control which led the parent to drink, rather than the inheritance of the effects of the drink on the parent. For in many cases a parent may not become a drunkard until after the children who also become drunkards are born. That the tendency to drink immoderately is frequently due to a strain of feeble-mindedness or epilepsy becomes more evident every day. In many of the so-called "periodical" drunkards, the accompanying features of their periodic attacks of drink-craving, such as clouding of memory, restlessness and depression, are those commonly associated with ordinary epileptic attacks.

Probably over Fifty Per Cent. of Inebriety in Man Due to Defective Nervous Constitution.—Branthwaite, an English authority on drunkenness, finds that about sixty-three per cent. of the inebriates who come to his notice are mentally defective. In alcoholic insanities heredity is a potent factor. It is coming to be realized more and more that pronounced alcoholism is due in a large percentage of cases, perhaps over half, to a defective nervous make-up. While it is true that many drunkards would not develop without free access to alcohol, on the other hand many would never develop without a bad heredity back of them, which gives them a peculiar nervous constitution that renders alcohol an undue stimulus. In a recent report of the New York State Hospital Commission it is stated that in fifty-four per cent. of the cases of alcoholic insanity, a family history of insanity, epilepsy or nervous disease exists. Thus in the presence of alcohol most of these unfortunates are helpless pawns of a hereditary weakness.

So when the question of alcoholism is viewed from all angles, the children of the human drunkard would seem to run a double menace of misfortune, since they may be subject both to the direct poisoning effects of alcohol and the results of an inheritable degeneracy.

Factors to be Reckoned with in the Study of Alcoholism.—In any thoroughgoing study of alcoholism in man many factors will have to be reckoned with. First of all there is the question

of inherent lack of control. This is probably the principal thing inherited where heredity truly enters as a factor. That example and social environment are important factors in addition to or in place of heredity is clear, too, when we observe that often it is the boys only who take after a drunken father, for there is no evidence that the inherited tendency when it really exists is at all sex-linked. Again, in certain occupations carried on under unwholesome influences relief is frequently sought in alcoholic stimulants, and such custom may easily crystallize into habit. Furthermore, the accustoming young children to doses of alcohol, or the unborn young to alcohol through the body of a drunken mother, may be strongly contributory toward establishing inebriety in certain cases. As we have seen from Stockard's experimental data on guinea-pigs, moreover, the nurture effects on germ-cells may result in the production of weakened offspring. Such offspring in the case of man are probably less able to withstand temptations of all kinds and hence readily succumb to the habit-forming effects of alcohol if once its use is begun. Lastly, it must not be forgotten that alcoholism in the father usually means poverty and the subsequent accompaniment of malnutrition and neglect of the children, and this in itself may not only account for poor development of the latter, but may also be strongly contributory toward establishing the habit of alcoholism in them.

An inherent bias plus most of the other conditions just enumerated is the not unusual lot of the offspring of drunkards.

VENEREAL DISEASES

There is yet another very considerable class of maritally unfit who in any conscientious discussion of unfitness for marriage or of racial improvement must be considered. I refer to those who are afflicted with the diseases which are inseparably associated with the so-called "social evil."

Prevalence of Venereal Diseases.—As to the prevalence of venereal diseases our knowledge is very incomplete. We have a certain amount of information on particular classes, but little on the population as a whole. It is obvious that tests on a group of supposedly healthy men would show a smaller percentage of cases than tests applied to a group of sick men such as one finds in hospitals, and that averages found for men in

general would be far too high for women and children. Moreover, the prevalence undoubtedly varies in different parts of the United States and is not the same in urban and rural communities. Lastly, studies made in St. Louis, Baltimore, and elsewhere, show that in America syphilis is from two to three times as prevalent in the negro as in the white race.

After pointing out that from twenty-two to twenty-five per cent. of the patients entering Bellevue Hospital give positive reactions when tested for syphilis, a monthly bulletin of the Department of Health of New York City in 1915 expressed the belief that proper tests applied to the public at large would show that one-tenth of the adult population of New York City is syphilitic. Estimates such as this based on the number of syphilitics who enter a public charity hospital like Bellevue are probably unfair to the general run of citizens of New York. Nor can the exaggerated guesses made a few years ago by certain specialists in these diseases be regarded as trustworthy. Encountering an inordinate proportion of such maladies every day, as the specialist does, his estimates are obviously likely to run unduly high for the public at large.

Facts published by the Surgeon General's office, based on the examination of two and one-half million men during the late war, show that at the time of medical examination there was an average of fifty-six per thousand infected with venereal disease of some kind; in other words 5.6 per cent. But unquestionably this average was swollen greatly by the inclusion of the negro troops of the Southern States. Recruits from Florida, for example, showed 16.3 per cent. of infection, and not one of the Southern States showed less than 10 per cent. The rates for representative Northern States were as follows: Vermont, 1 per cent.; South Dakota, 1.6 per cent.; Massachusetts, 2.4 per cent.; New York, 3 per cent.; Utah, Oregon and Wisconsin, each 2 per cent. This is the best sample of conditions at large in the general population of the United States that has ever been obtained and even with a liberal addition for latent and undetected cases the proportions would not reach anything like the estimates current a few years ago. A recent special medical examination in one of our large universities in the Central States showed that only twelve out of four thousand men were afflicted with venereal disease. This is a far better record, of course, than would be found among the same number of individuals

of the same age chosen at random from our general population.

It is the opinion of many instructors in colleges and universities who have associated for years in more or less confidential capacities with men students that there is much less venereal disease among the college students of to-day than formerly. This is indicative that the active educational campaigns of the past two decades relative to the dangers of venereal diseases are bearing fruit. The results would naturally be observed first among the better instructed classes. While the general public has never before been so well informed in the matter, and as a result there is probably somewhat of a decline in venereal diseases, much yet remains to be done to reach the great masses of people.

One great cause of ignorance in the past was the prudish taboo against frank discussions of such diseases which has thrown the veil of silence about the subject. To-day, however, it is coming to be recognized that these maladies are diseases and not a standard of social propriety, and that like most other diseases the surest way to secure prevention and gradual eradication is through the enlightenment of the public. Moreover, it must not be forgotten that there is no form of venereal disease which may not be innocently acquired. Even where acquired through transgression of moral law an ignorant attitude toward the sexual instinct is often at the bottom of the difficulty. Physicians and sanitarians already know enough about the causes, prevention and cure of venereal diseases to insure their sanitary control and gradual eradication if public opinion would permit of the practical application of this knowledge. Unquestionably the backwardness of public opinion and the unfortunate confounding of this sanitary problem with questions of morals are the chief impediments to bringing these diseases under control.

While any one who has progressed in worldly knowledge beyond the naïveté of a child must recognize the fact that these maladies are common, nothing is gained through grossly exaggerating conditions by pointing the finger of suspicion at from one-third to one-half of our adult male population. Surely dramatic heightening is unnecessary to render the situation impressive.

Infantile Blindness.—To gonorrhea, one of the most prevalent of these diseases, more than one-fourth of our total blind in the United States are said to owe their affliction. Milder

types of eye disease may also result from such infections. From fifty to eighty per cent. of the blindness in young children is caused by it, the infection occurring at the time of birth or within a few days thereafter. So serious has the matter of infantile blindness become that some state boards of health and some city health departments supply all physicians and midwives with specially prepared packages containing cotton and nitrate of silver solution for preventive or curative treatment of the eyes of all new-born children. At the time of the first bath each eye is carefully washed with a separate pledget of cotton saturated with boric acid solution. Each then receives a drop of the silver solution, which is made just strong enough to kill any gonococci that might be present without itself inflaming the eye. Water used in bathing the baby's body of course is not allowed to come in contact with its eyes. Such treatment should be given every child no matter how unsuspecting the circumstances may be. German authorities who have been following this method now for some years assure us that nineteen-twentieths of the blindness of infancy can thus be prevented.

Seriousness of Gonorrheal Infections.—Unfortunately the insidious nature of gonorrheal infections is unknown to most persons. A cure is apparently effected, yet as a matter of fact the germs may live for years and, if in the male, later be transmitted to the wife, subjecting her to a future of invalidism and misery. Seventy per cent. of the women who come to the New York Hospital for treatment of venereal diseases are respectable married women infected by their husbands. Statistics from various medical authorities reveal the appalling fact that some eighty per cent. of the serious inflammatory diseases peculiar to women which often necessitate hazardous operations and frequently result in death or permanent invalidism, are attributable to gonorrhea as is also the involuntary sterility of forty-five per cent. of childless women.

Syphilis.—As to syphilis, another and even more terrible of these diseases, we have before us the absurd fact that while thousands upon thousands of dollars are being spent to establish a rigid inspection and preventive measures against the spread of a very similar disease in the horse, this malady in man is allowed to pass largely unchallenged in most states and we are confronted by the gruesome certainty that there are many of these diseased persons about us to-day who, on their mere

affirmation that they are unmarried and of age, will be given the right to marry and thus produce families of infected children irrevocably doomed to early death or to lifelong misery.

Syphilis is caused by *Treponema pallidum*, a small unicellular animal parasite. Given access to the blood by any means whatever, possibly even through an abrasion in the lip by means of a kiss, it multiplies rapidly and any part or organ of the body may be attacked. Usually a small sore occurs at the point of entrance to the body, but often it heals up readily and with little indication of the seriousness of the infection.

The development of the malady is insidious and long continued. As a matter of clinical convenience physicians divide its progress into successive stages although in reality the transitions are frequently variable and ill marked. The symptoms that arise within the first few months or even years are readily controlled by appropriate treatment, but to insure a cure prolonged and most thoroughgoing treatment is imperative. The symptoms disappear so completely after a short period of treatment that it is very difficult to persuade the average patient that he is not yet cured. Two years at least are none too short a period of treatment, yet the majority of patients, fully convinced that they are merely being exploited by the physician as a source of revenue, drift away at the end of a few months. As a matter of fact, however, the germs usually persist long after the obvious symptoms of the disease have disappeared, and in consequence many of the most serious results of syphilis may not manifest themselves for a period of perhaps ten, twenty or thirty years.

Some of the Effects.—It is now known that *Paresis*, also termed general paralysis or softening of the brain, is probably invariably due to syphilis. The work of Flexner and Noguchi on *paresis* and *tabes dorsalis* show that always in such afflictions the tissues of the central nervous system have been invaded by the parasite. The original infection, however, may have occurred so long before as to have been almost forgotten by the patient. Thus many an apparently robust man is stricken down in the prime of life. Earlier and prolonged treatment would in all probability have eradicated the germs and thus prevented the mental breakdown, which can not be cured by any known treatment. Post-mortem examination always shows that the *Treponema* has wrought wide-spread damage in the brain. The frequency of paresis may be realized when one learns that in some

regions it is responsible for about one-fifth of all cases of insanity sent to hospitals for the insane. It ranks next to the highest as a cause of insanity. Statistics show that in the state of New York more deaths result annually from paresis than from smallpox, tetanus, malaria, dysentery and rabies all combined.

In some cases the disease attacks the membranes of the brain and the small blood-vessels giving rise to a still different type of mental disorder. Practically all patients with *locomotor ataxia* owe their condition to an antecedent syphilis. Moreover it is one of the important causes of *arterio-sclerosis*, or hardening of the blood-vessels, and is also a prominent factor in certain forms of heart-disease, as well as by no means an unimportant cause of blindness in children.

We are learning that much general impairment of health is due to an earlier infection of syphilis and that it is an important factor in producing thousands of disabilities and deaths that were formerly attributed to other causes. According to British statistics thirty-three per cent. of deafness in young people is due to syphilis, and the American Social Hygiene Association reports that fifteen per cent. of all first admissions to the New York State Hospital for the insane are traceable to syphilis. It is estimated that about twelve per cent. of the total insanity in the United States was caused by syphilis.

Effects of Syphilis on Offspring.—Improved diagnosis shows that the transmission of syphilis to offspring is far more common than was previously thought. Studies by Jeans show how important it is to investigate the other members of each patient's family. Numerous cases of latent syphilis may thus be unearthed. Many pathological conditions in children of which formerly the causes were obscure are now known to be the result of syphilitic infection. Not only is there a waste of potential citizens by miscarriage and death twice as great in syphilitic families as in similar families which are not syphilitic, but the children which survive are likely to be shot through and through with organic defects and degenerative changes. Congenital syphilis operates most profoundly, perhaps, through markedly harmful malnutrition, although it is not infrequently accompanied by other pathological conditions. Of the many different ills which may result, often tardily, from this infection, in children, the most usual perhaps are affections of the central

nervous system, bones, joints, eyes and skin. In spite of recent statements, based on defectives in institutions, expressing doubts as to a causative connection of syphilis with feeble-mindedness, careful clinical tests by Veeder on one hundred children who manifested the result of so-called "tardy" syphilis, showed approximately one-fourth to be mentally deficient. Jeans and Butler found five times as much feeble-mindedness in syphilitic as in non-syphilitic families of the same class. While it is seldom clear just which is cause and which effect in such cases, it is a noteworthy fact that syphilis and feeble-mindedness often go hand in hand.

A Blood Test.—Fortunately a blood test known as the Wasserman test has been discovered by means of which, through an examination of a few drops of blood, the presence of syphilis in the body may usually be detected. This is true even though the individual may at the time show no visible symptoms of the disease. The test is therefore of great value in detecting the latent germs of syphilis in individuals who have apparently been cured, and also often in making an early diagnosis of paresis. The Wasserman test, however, is reliable only in the hands of a skilled operator. It may occasionally give a positive reaction when syphilis does not exist and on the contrary a negative when it is present. In suspicious cases which give only negative results by an ordinary Wasserman, other tests are available.

Many Syphilitics Are Married.—It may seem to some that in a treatise on being well-born the subject of syphilis might be ignored as not being especially pertinent, but the supposition that no considerable percentage of syphilitics marry is not borne out by the facts. Seventy-five per cent. of men with insanity due to syphilis who are admitted to hospitals are married. The insanity in such cases is mainly the result of infections in earlier years, often long before marriage. While syphilis, strictly speaking, is not inherited, that is, does not become part and parcel of the germ-plasm, still the frequency of its direct transmission to offspring is so appalling that the outcome, as far as the immediate child is concerned, is quite as disastrous as the most thoroughgoing real inheritance could be.

Sources of Venereal Infection.—The great source of infection is prostitution. Practically every prostitute is a center of dissemination and there is a steady procession of these diseases from the women of the street to the women and children of

the home. According to The American Social Hygiene Association careful investigations show that 98 per cent. of white prostitutes have at least one venereal disease; that 90 per cent. of all syphilitic infections in men are derived from prostitutes; and that 85 per cent. of married women who have syphilis have contracted it from their husbands. Although the venereal diseases are most commonly spread through relations of the sexes they may be acquired in various other ways. Thus syphilis has often been contracted through a cut in shaving, by means of kissing, or from articles of the kitchen or toilet used by infected people, and gonorrheal infection of the eyes has often resulted from transmission by means of towels or wash basins.

Why Permit Conditions to Continue as They Are?—When one faces the easily ascertained facts regarding venereal disease, it seems incredible that we, an intelligent people, can go on complacently handing our daughters and sisters over to the surgeon's knife and a life of personal misery, and even in not a few instances to become mothers of incurably defective children, yet the dire fact confronts us that we do. We can no longer excuse ourselves on the plea of ignorance, for the grisly record may now be read in many medical and not a few popular treatises, and we find the theme entering even into the modern drama, as witness Brieux's *Damaged Goods*. Further indifference to these conditions can only be attributed to culpable apathy or prudery.

The extreme dangers to which parents are subjecting their daughters if they do not demand a clean bill of health on the part of their prospective husbands are obvious. Fathers and mothers perfectly willing to inquire into their future son-in-law's social connections, his income, securities, or business chances become strangely "modest" when it comes to determining whether he is physically fit for marriage.

Medical Inspection before Marriage.—Pre-nuptial medical inspection is certainly as necessary to the welfare of society as the certification of age and of the single state now required by law. No one objects to a medical examination pertaining to venereal and other diseases when it comes to taking out a life insurance policy, and why there should be any more objection to it as a preliminary to marriage is a mystery. Some states already have compulsory pre-nuptial medical inspection. In Wisconsin, where such a law has been in effect since January 1,

1914, the public seems on the whole to be in favor of the provision. At least one hears much favorable comment and little dissension among those who understand its purpose. The very controversy over it which sprang up after its passage proved to be of great benefit in the education of the public regarding the necessity of such measures. Such physicians as I have been able to question report that the candidates for marriage rarely object to the requirement, but on the contrary strongly favor it. Especially where they have suffered from venereal disease earlier in life most are eager to know their condition and to have medical advice. To my own mind this last fact is the most significant of all, as it will give every candidate for marriage a chance to know the truth. Most men are not so much brutal or vicious as ignorant in such matters. The vast majority of those unfit for marriage as a consequence of venereal disease will, when they realize the danger their condition imposes on wife and children, take every possible means to put themselves into proper condition.

The Perils of Venereal Disease Must Be Prevented at Any Cost.—However, no matter what the cost may be to the state, no matter what the exaction from the individual, the grave perils of venereal disease to society *must* be prevented. We owe it to the cause of humanity that there be fewer victims born into a world of eternal night, that from a parentage of polluted blood there spring no longer hosts of children with feeble, misshapen bodies or with tarnished intellects, death-marked at the door of life.

Treatment.—It should be well understood by every one that syphilis is usually curable provided the patient is given modern scientific treatment by a *competent* physician. I emphasize competent because there are so many quacks in this field that one undergoing treatment can not be too careful in assuring himself of the competency of the physician. In even a case of long standing, where the symptoms have been in abeyance for a number of years, the disease can be cured provided it has not developed into an active cerebro-spinal type, and even the latter can be much benefited by proper treatment. The great danger of the cerebro-spinal type is that it will result in paresis or locomotor ataxia.

As long as the blood of a patient shows a *positive* Wasserman reaction, marriage should certainly not be consummated. If after

a proper course of treatment by a well-informed physician, the patient shows a *negative* Wasserman when tested by a competent examiner, he probably would not infect his wife or offspring, although prudence would require that he wait at least six months or a year before marriage, and marry then only if later tests remain negative.

The only way for a patient to be sure that he is not harboring the cerebro-spinal form would be to have a spinal puncture made and the cerebro-spinal fluid examined. While the cerebro-spinal phase often does not occur until long after the primary infection, cases are known in which it has appeared within a few weeks. Evidence that the central nervous system is frequently invaded early in the course of the disease is increasing. Marriage of an individual suffering from the cerebro-spinal form should not take place, since such a one is almost sure to become a burden on the family or the state.

With children as with adults the importance of early diagnosis can not be over-emphasized, since treatment of the infantile type is hopeful, while therapeutic results on the "late" transmitted form are likely to prove disappointing. Jeans and Butler found that thirty-three per cent. of syphilitic children over thirteen months of age showed permanent disabling damage of the nervous system and eighteen per cent. long continued disabling impairment of vision.

Urgent means are needed to compel treatment of luetic children. It is a common experience in clinics that many never are returned after the initial visit or are brought for a short period only, possibly until the acute symptoms are cleared up. This keeping of the clinic and the home in contact is a function that might well be exercised by some sort of a social service department. The St. Louis Children's Hospital has been able to get compulsion into effect through the Juvenile Court on the ground that syphilitic children not under treatment can be brought into court as "neglected children." The knowledge that treatment could and would be enforced through the court, if necessary, usually brought indifferent or recalcitrant parents to time because they feared the publicity which might attend appearance in court.

Since an enlightened public opinion is an indispensable preliminary to further progress strong and persistent efforts should be devoted to the task of education. The greatest advancement will be secured through a frank, unsentimental, scientific statement of the facts to the people. The importance of early diag-

nosis and intensive treatment as well as the appalling results of neglect can not be too strongly emphasized, nor can the necessity of continuing treatment until the patient is completely cured.

In addition to the lecture and exhibition methods now in vogue much good can be done by preparing educational placards and having them placed, by law if necessary, in public and semi-public toilets used by men, such as those of hotels, boats, barber shops, railway cars and stations, stores, factories and shops. To give them the necessary weight of authority and to combat quackery such cards should bear the signature of the City or the State Board of Health. They should drive home their message by the use of non-technical language, short sentences and emphasis of type. Boards of health could advertise in the newspapers to advantage. Judging from the profusion of notices to be found in such papers as accept the advertisements of so-called men's specialists and quack nostrums, a large and impressionable audience should be reached by this means. Some departments of health, in fact, such as The New York City Board of Health, are already using the agency of newspapers.

As to legislation, without disparaging in the least what has been done in the various states in a more or less experimental way, it may be said that those forms of legislation which grant state and municipal boards of health power and funds to establish what in their experience may prove to be wise regulations, are preferable to direct legislative enactments aimed at physicians and patients individually. Any law or regulation will be successful just in the proportion that the patient sees it is for his own good. While it is highly desirable to have a record of every case treated by physicians reported to some central bureau, no successful method of accomplishing this end has yet been devised. So greatly is the scandal of publicity feared by venereal patients that attempts to enforce so-called "reporting" laws will drive such patients from honest physicians who report, to quacks and proprietary medicines. If merely the number of patients treated is reported without name, then little accurate information is gained because even if all physicians can be induced to report, since such patients make frequent changes, the same individual will be reported repeatedly by different physicians and institutions.

It is imperative that it be made easy for those suffering from venereal diseases to secure advice and treatment. To this end every state should have thoroughly equipped laboratories in which diagnosis of venereal diseases shall be made free of charge to

physicians or patients. This is already the practise in some states. Such institutions should be equipped not only to make routine Wasserman tests but such supplementary and corroborative tests as atypical or obscure cases may necessitate. It is clear, moreover, that states and cities must assist physicians more and more, not only in diagnosis but in helping to provide the more expensive forms of treatment.

While for the indigent there must be free treatment or treatment at a nominal fee at public dispensaries, there should also be beds for venereal patients in general hospitals. If all such patients are compelled to go to special institutions, then, because of the social stigma, many who should have treatment will conceal their condition and suffer the appalling results of neglect. The absurdity of hospitals refusing to admit patients avowedly suffering from venereal disease is evident since it has been shown in several hospitals which now perform a Wasserman reaction on all patients, that from fifteen to twenty-five per cent. of patients admitted for other causes are syphilitic.

The Wasserman test should become a routine matter in every public hospital, prison, workhouse and institution for delinquents, insane or feeble-minded, at least, and it might well be insisted on for such venders and servants as come into close contact with food materials.

Bad Environment Can Wreck Good Germ-Plasm.—In conclusion it is evident from our discussion of prenatal influences that not all of being well-born is concerned with heredity in its proper sense, since the unborn young may be influenced either directly or indirectly by environmental conditions which are in no sense products of heredity, although as far as the immediate child is concerned the result may be quite as disastrous where the influence is a baneful one. As to the production of beneficial prenatal effects, while parents can do nothing toward modifying favorably such qualities as are predetermined in their germ-plasm, nevertheless they must come to realize that bad environment can wreck good germ-plasm. They can see to it that they keep themselves in good physical condition by wholesome temperate living, and thereby insure as far as possible healthy germ-cells for the conception and good nutrition for the sustenance of their progeny. Their one sacred obligation to the immortal germ-plasm of which they are the trustees is to see that they hand it on with its maximal possibilities undimmed by innutrition, poisons or vice.

CHAPTER XVIII

HUMAN CONDUCT

"Out of the dusk they troop, my son, from the uttermost pales of the Past,

Your brawn is theirs and your brain is theirs; you do as they bid you do.
The urge of a million sires and dames in the blood of your pulses runs,
As your own urge will some time surge in the sons of your children's sons.
In weird array the grim and gay, the priest and the pagan ride;
The knight with the knave, the king with the slave and the wanton, side by
side.

Out of the dusk they troop—a wild, fantastical masque of man,
As we shall ride in the blood of our sons in the fantom caravan.

Their prides are yours; their loves and their lusts, their hopes and their hates are your own;
You are the fruit that their loins have bred, the flower of the seed they have sown."

—Kendall Banning.

Since both physical and mental attributes are unquestionably inherited, it becomes a matter of importance to inquire into the nature of the entity we call personality. To what extent is human conduct a product of parentage? Although apparently free agents, are we in reality only by infinitely subtle indirections making the responses, forming the habits, establishing the characters which result merely from the blind impulses of an inherent constitution? If so, who is praiseworthy, who blameworthy? Are men

“But helpless pieces of the Game He plays
Upon this chequer-board of Nights and Days.”

All Mental Process Accompanied by Neural Process.— Whatever the ultimate decision of psychologists may be regarding the relation of mind to the sensory and nervous mechanism of man, it is certain that there is so close an association between them that the least alteration in the mechanism means a parallel effect in the mind, or in the words of Huxley, "every psychosis is definitely correlated with a neurosis." The rind or *cortex* of gray matter which constitutes the surface of the large cerebral hemispheres of the human brain is regarded as the seat of the

more complicated intellectual and voluntary adjustments. The development of the mental powers in the infant is dependent on the development of the elements of this cortical substance and the waning of the mental faculties in old age goes hand in hand with its atrophy. Abnormal arrangements, injuries or omissions in it mean mental unsoundness. How the activity of the structural mechanism gives a reaction in consciousness is not understood, but we know that in the living being the two phenomena are inseparably linked. Whether we accept the hypothesis that consciousness is an actual product of the structural mechanism or the hypothesis that the latter is only an instrument for the manifestations as consciousness of an outside force or entity, just as the telegraphic instrument manifests the existence of electricity, is neither here nor there for our purposes. On either supposition the degree and manner of expression are determined by the structure of the mechanism. Our main problem is to decide as nearly as possible how much of the mechanism is rigidly inherited, how much is at birth largely undetermined, so that its ultimate outcome is in part a product of the forces which play upon it, or in other words of education and training.

Gradation in Nervous Response from Lower Organisms to Man.—To comprehend fully the basic nature of human neural responses one must seek the roots in the behavior of lower organisms. For there is found in a simpler form many of the fundamental activities and the first dim gropings which emerge in man as memory, reason and will. As we ascend the scale of animal life we find a continuous advance in neural complexity and nervous response that in many respects grades up closely to the human type.

Behavior of Many Animals Often an Automatic Adjustment to Simple External Agents.—A windmill or a weather-vane points toward the source of the wind, obviously not because either exercises any special choice in the matter, but because it is constructed on such lines of symmetry that when the wind strikes it, if it slants the slightest to left or right, the more exposed surface receives the greater pressure and thus swings the body back into the line of least resistance.

It is a far cry, of course, from the responses of such a machine as a windmill to the responses of even the simplest living thing, but in spite of the broad gap between the two, there is much reason to believe that the behavior of many living organisms is

due in a marked degree to the directive effects of comparatively simple external factors rather than to the complex internal volitions the casual observer is likely to attribute to them.

Tropisms.—It is a marked characteristic of all living protoplasm that it has the power of responding to external stimuli. This power of response is termed *excitability* or *irritability*. In describing the motor responses of living organisms to stimuli resulting from a change in surroundings the term *tropism* (Gr. *Tropē*, turning), is frequently used and the kind of stimulus is indicated by a prefix. Thus the term phototropism means a turning or *orientation* brought about by means of light. An organism which reacts by a movement toward the source of light is said to be *positively phototropic*, one which moves away from it, *negatively phototropic*. By using such a neutral terminology the physiologist avoids implying that necessarily “likes” or “dislikes” or any other psychic reaction enter into the movements.

Several kinds of tropisms are recognized, such as *phototropism* or *heliotropism*, reaction to light; *thermotropism*, reaction to heat; *electrotropism* or *galvanotropism*, to electric current; *geotropism*, to gravity; *chemotropism*, to a chemical; *rheotropism*, to current; *thigmotropism* or *stereotropism*, to contact; and *chromotropism*, to color.

Many Animals Show Tropic Responses.—Many of the lower animals seem to have their movements determined more or less mechanically by the action of such external factors, some being positively, others negatively responsive to a given kind of stimulus, or the same individual may be at one time positive, at another negative, according to modifying conditions to be mentioned presently.

In plants and in simpler lower animals there is no special nervous system. The responses of these organisms depend on the general irritability of their constituent protoplasm. In other animals a nervous system is developed, crude and diffuse in lower forms, extremely delicate, complex and definitely ordered in higher forms. But it should be borne in mind that nerve protoplasm possesses only in high degree a capacity for irritability, conduction, etc., that is common to all living substance. In keeping with other “physiological division of labor” or specialization which marks the increasing complexity of animals, this enormously enhanced sensitivity and conductivity of certain tissues has come about, and they have become set apart for

these special functions. In higher animals, therefore, the tropisms where operative must act more or less through the agency of the nervous system instead of directly through the general protoplasm of the organism.

Certain Apparently Complex Volitions Probably Only Tropisms.—Where nervous systems enter into tropic responses there must be specific sensibility of certain nerve terminations (i. e., sense organs) at the surface of the body. These sensory or receiving nerves connect through the central system with corresponding motor nerves which in turn supply certain specific muscles through the contraction of which the organism is as surely and as mechanically oriented as in the simpler cases. For example, if light is the stimulating agent, when it strikes a positively phototropic animal, if the latter is not already oriented, the eyes or other nerve terminations sensitive to light transmit an impulse through the central nervous system to certain muscles causing them to increase their tension and thereby swing the animal around with its head toward the light. Progressive movements which the organism then makes must carry it toward the source of light. Thus it is not "love of light" that draws the moth into the flame but the mechanical steering of the body toward the source of light through the stimulations produced by the light waves. It is chemotropism, not solicitude for its offspring, which drives the flesh fly to lay its eggs on decaying meat. And it is stereotropism and not a desire for concealment which impels certain animals such as many worms and insects to get into a close contact with solid bodies, or in other words to "hide" themselves in burrows and crevices.

Complicating Factors.—However, beautifully as these theories of tropisms work out in a broad general way, there are various additional factors entering which must be reckoned with, and these become more numerous and of more consequence as the organism becomes more complex. In the first place certain internal conditions must be considered. Living matter is characterized by its instability. There are continual synthetic and disruptive processes in progress which the physiologist terms metabolic changes. The very "life" of such matter seems to be the manifestation of such changes. Concerning what the ultimate source of these changes is, whether or not indirectly they may be referred to external conditions as seems probable to many biologists, no one so far has ever given a convincing, positive

answer. It is sufficient for our purposes to know that they may have set up certain internal stimuli which may modify the behavior of the organism in which they reside, and that the "physiological state" of the organism at the time of external or internal stimulation will condition the response. This physiological condition may be dependent on the general metabolic equilibrium of the animal, or on the extent of previous stimulation by means of the same or different agents. Thus the organism may not always react in the same way to the same stimulus.

The intensity of the stimulation and change in the intensity of the stimulation, are also factors to be reckoned with. Moreover, it must be taken into account that a given organism is often operating under the control of more than one external influence. For example, swarm spores, in a dish of water which at a given temperature are positively phototropic, that is, tend to gather at the side of the dish toward the light, may, if the temperature of the water is raised or in case of marine forms if the salinity is increased, become negatively phototropic. Sometimes two or more forms of stimuli may cooperate in bringing about certain behavior as, for instance, in the reaction of the earthworm to a suitable habitat, through a combination of chemical and contact stimuli. On the other hand, two different stimuli may interfere with each other; for example, the usual phototropic responses of certain animals do not manifest themselves when they are mating or feeding. In short, anything that alters the physiological state of the organism may cause it to react in a different manner. And thus with the interplay of shifting external agents and variable internal states the bounds of behavior on these purely mechanical bases become considerably extended.

Many Tropic Responses Apparently Purposeful.—The query arises as to why if these responses are mechanical they are so often apparently purposive; that is, why do they so often subserve some useful end for the animal? While they do not always work out to the animal's benefit, as for instance in the case of the moth and the light, or under many other conditions that can be devised experimentally, as a matter of fact under normal natural conditions they are on the whole useful to the organism, carrying it into suitable surroundings of food, lessened danger, temperature, and the like.

The probabilities are that in their first origin the reactions were

not purposive. However, if any proved harmful they would result in the extermination of their possessors and hence of that particular strain of individuals. Those types that happened to have useful reactions would be left and in course of time as the process of eliminating the others went on, would become the prevailing types. Any organism which the useful reaction had preserved would tend to hand it down to the succeeding generation where again it would be the conserver of those individuals which possessed it in sufficient degree.

Authorities Not Agreed on Details of Tropic Responses.—Although all the foremost modern students of animal behavior accept as facts the more or less mechanical orienting effects of external stimuli, there is by no means unanimity of opinion regarding details. Some stress as the directive factor the continuous action of the stimulating agent on sensitive tissues symmetrically situated. Others would maintain that it is the time rate of change in the intensity of the stimulating agent, or that the factor is different in different cases. Some make much of an automatic sort of "trial and error" system by which certain organisms test out an inimical environment until the path of least irritation is hit upon as the way to safety. The field is a broad one and to get at the finer shades of distinction the reader will have to refer to the works of such authorities as Loeb, Jennings, Holmes and Mast.

Tropisms Grade into Reflex Actions and Instincts.—The tropisms in many cases become indistinguishable from *reflex actions* and these in turn grade up into the *instincts* of animals. The latter may be looked on as but subtler and more involved reactions made possible through a more intricate structural organization. As might be expected of instincts, the feature of utility is more in evidence than in simpler tropisms because they have become of proportionately greater magnitude, but the same fundamental mechanism is apparently at bottom of both. It has already been seen how the "instinct" of the blow-fly to lay its egg on meat is interpretable as a chemotropic response. Thus no elaborate psychic mechanism is necessary in such behavior.

Instincts.—The term instinct has been so abused by inaccurate usage that it has become almost valueless for scientific precision. Careless writers confuse the innate stimulus-response types of adjustment compounded of simpler reflexes, which alone should be reckoned as instinct, with what are clearly acquired

habits, intelligent action, or in some cases even mental or moral abstractions. Instincts are not entities which can be inherited in terms of social or ethical meaning since such meanings are conceptual and relative, not absolute. Even naming instincts in terms of the response observed leads into difficulties since the same action-pattern may serve more than one end. Both instincts and habits are manifested as machine-like non-intelligent behavior and unless one knows the origin and history of such activities they are often indistinguishable, hence it is little wonder that they are frequently confused. The habit-forming powers of man, in particular, are so great that unquestionably much of his behavior which at first sight looks instinctive is really a series of acquired reactions, or in other words, habits operating on a substratum of instinct. Unquestionably, however, the existence of the instincts makes it far easier to establish habits in harmony with them than otherwise.

There is no hard and fast distinction between reflexes and instincts. In general where the inherited action-pattern is more complex than that involved in a simple direct stimulus and response, the reaction, particularly if more or less definitely directed toward a useful end, is usually regarded as an instinctive one. In the typical instinct there is a series of "chain reflexes" in which one step determines the next until mechanically the whole gamut of changes is run to the last step. It is characteristic of a purely instinctive act that an animal performs it without practise, without instruction, and without reason. Moreover, all of the same kind of animals tend to perform the act in the same way. However, with instincts, as with tropisms, the physiological state of the organism must be regarded. For instance, the instinctive reactions of an animal sated with food or hungry will be different.

Adjustability of Instincts Opens the Way for Intelligent Behavior.—As we progress in the scale of animal life this adjustability of instincts to new conditions comes more into evidence. While prescribed in the main by internal impulse the carrying out of the action is capable of some adaptability to circumstances. And in proportion as this adaptability releases the organism from a blind working-out of a predetermined end, there is opened up the possibility of intelligent behavior; that is, of modification of the instinctive behavior by individually acquired experience.

While the generation of instinctive impulses still occurs it is left more for individual experience to teach discrimination between ends. But we can not escape a fundamental structural mechanism, for with this new capacity of educability must come new structural mechanisms in the nervous system and this must be as faithfully reproduced in each individual as is the basis for any other nervous response. How low in the scale of animal life animals can profit from their experiences to the extent that their future conduct is conditioned thereby is not known. Some would place it as far back as the protozoa, others would not. Where such modification of behavior is possible there must be some mechanism for the storage of impressions in the form of what we term *memory*.

Modification of Habits Possible in Lower Animals.—Among invertebrates such animals as crayfish will acquire new habits, or rather will modify old ones. Even as lowly an organism as the starfish can have changes of habit thrust on it. When a starfish is placed upon its back it rights itself by means of its arms or rays. Professor Jennings found that in a given individual the tendency was always to employ certain rays for this rather than others. However, by preventing the use of the rays customarily employed, he found that the animal would use a different pair and that ultimately in this way it could be trained into the habit of using this pair of rays even when restrained in no way. One starfish which was given one hundred eighty such lessons in eighteen days after an interval of seven days still retained the new habit; young individuals were found to be more easily trained than old ones.

Some Lower Vertebartes Profit by Experience.—Among vertebrates it is known that those as low in organization as fish will profit by experience. They will learn to come for food at a regular time and apparently learn more or less to appreciate the presence of certain obstacles with which they have had unsatisfactory experiences. Professor Sanford sums up what he believes are the limitations of the piscine mental organization as follows: "No fish is ever conscious of himself; he never thinks of himself as doing this or that, or feeling in this way or that way. The whole direction of the mind is outward. He has no language and so can not think in verbal terms; he never names anything; he never talks to himself; as Huxley says of the crayfish, he 'has nothing to say to himself or any one else.'

He does not reflect; he makes no generalizations. All his thinking is in the present and in concrete terms. He has no voluntary attention, no volition in the true sense, no self-control."

Rational Behavior.—Finally, however, out of these first dull glimmerings of intelligence as exemplified in the higher invertebrates and the lower vertebrates, which can modify behavior as the result of experience, come the still higher factors so dominant in man, of *rational* behavior. This higher mental process can realize the end to be reached and can deliberate on the means to be employed. By means of his *reason* man can overcome difficulties in advance by "thinking" out suitable schemes of action. Man stands largely alone in possessing the power to reason, although some of the other mammals, notably the other primates, possess the same attribute in a much less degree.

Conceptual Thought Probably an Outgrowth of Simpler Psychic States.—Is the capacity for such conceptual thought, however, which appears as the final efflorescence of complex neural activity something entirely new? Most students of comparative psychology maintain that it is not. Just as one kind of an instinct frequently grows out of another, so has this grown out of the complex of *psychic* states which preceded it. It apparently is the product of the increasing awareness on the part of animals of their neural processes and the outcome of these processes, which becomes more and more prominent as we ascend the scale of animal life. With the advent of associative memory the mind comes more and more to deal with attributes of objects instead of merely with each single concrete object as it presents itself, and these attributes being common to many objects, come to represent definite ideas which can be manipulated by the mind. Language, of course, has been an indispensable aid to man in this regard, for words become descriptions of facts and symbols of concepts, and thereby permit of abstract thought.

Capacity for Alternative Action in High Animals Renders Possible More Than One Form of Behavior.—With this modification of instinct by experience made possible, there comes at the same time, of course, the capacity for a rational instead of a purely instinctive behavior. This very capacity for alternative action opens up many new possibilities of behavior and together with the well-known fixative effects of habit, also the opportunity of permanently establishing certain ones. Thus it is obvious that a behavior toward which in a strict sense there can not

be said to have been an original specific tendency, can be developed. What was present in the first place was only a general possibility of the development of any one of several types of behavior. The final choice of the alternatives together with repetition makes it the habitual behavior of the individual. Of course it can be urged that if the selection of the type of behavior is left to the individual then the latter will operate automatically toward the various impulsions of its neural make-up and one path will be followed because of stronger inclination in that direction, so that the whole procedure is in the end the mere operation of an automaton. But however this may be in the individual left to itself, the fact is in man that the young individual is never left to itself and in the nature of things can not be, so that without entering into this troubled pool of controversy regarding freedom of the will, I wish merely to point out that the possibility of more than one form of behavior exists and that if one is more desirable than the others then this one can be chosen by the ones responsible for the training of the young individual and clinched fast by the agency of habit.

Intelligence, reason and habits, however, no less than instincts and tropism must have neural as well as psychical existence and we can not escape therefore the underlying mechanism.

The Elemental Units of the Nervous System are the Same in Lower and Higher Animals.—It is interesting to note that the fundamental neural mechanism which underlies the mental processes of higher animals is not essentially different from that which serves in lower forms. Although as animals become more complex their nervous systems have become proportionately larger and incomparably more intricate, still all the changes have been rung on the same basic neural unit, the *neuron* or nerve-cell (Fig. 89A, p. 317). The higher nervous system differs from the lower in the number, in the specializations and in the associations of these units rather than in possessing something of entirely different elemental structure.

Neuron Theory.—According to the prevailing modern conception the entire nervous system is made up of a series of units called *neurons*. Each neuron is a single cell with all its processes. The latter consist typically of short branching processes on the one hand, known as *dendrites*, and of a single process on the other, known as the *axon*, which extends from the cell to become a nerve fiber (Fig. 89, p. 317). The various neurons, with

possibly a few exceptions, are not anatomically continuous but contiguous. They communicate with one another apparently by contact only. The axon of each neuron ends in an elaborate series of fine branchings which lie in contact with the dendrites of another neuron, or in some cases with the body of the other cell (Fig. 89, below). Thus the nervous impulse passes from

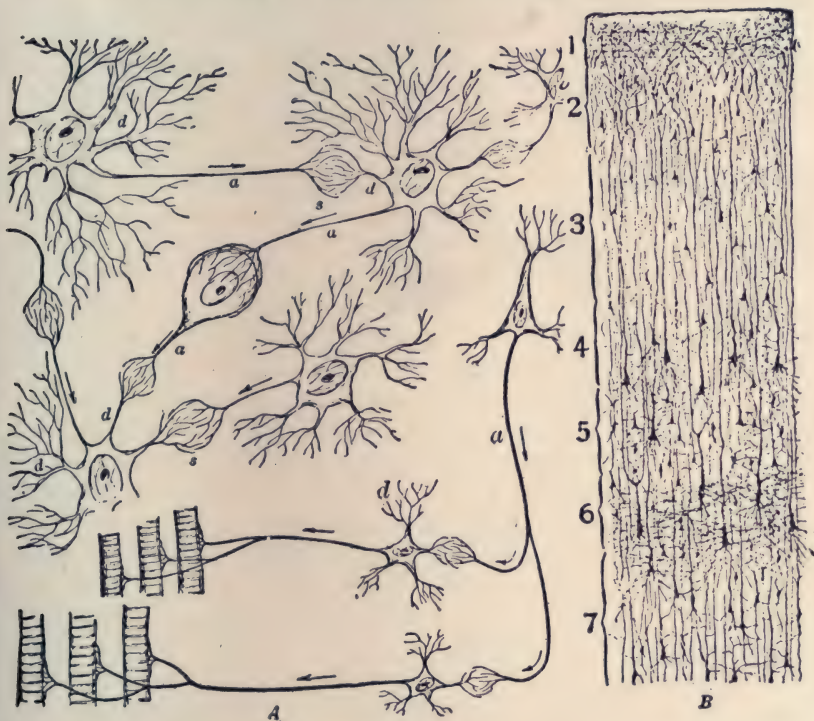


FIG. 89

A—Diagram to illustrate neurons and their method of connection; *a*, axon; *d*, dendrite; *s*, synapse. To simplify the diagram the medullary sheaths of such fibers as would have them have been omitted. The arrows indicate the direction in which the impulse travels. The lower series shows diagrammatically how from the same neuron in the cortex two subordinate neurons may be affected, the one excited to cause contraction of a certain group of muscle fibers, the other inhibited so that the antagonistic fibers may relax and thus not hinder the movement of a given part.

B—Section of a region of the cerebral cortex (after Cajal). The cells have been blackened with chromo-silver and are much less highly magnified than the diagrams in A. The numerals refer to certain characteristic layers of the cortex in this region.

one neuron to the other at these points of contact. An impulse is supposed to travel normally only in one direction through a neuron, the dendrites being the receiving and the axon the discharging terminals. There are various types of neurons. Some, particularly within the brain, have their main processes so provided with branches and brushes that they may come into physiological connection with a number of other neurons.

Establishment of Pathways through the Nervous System.—

It is believed that more or less resistance to transmission of stimuli prevails at the point of contact (*synapse*) between two neurons but that this resistance is lessened by repetition of conduction. The frequent traversing of a given pathway by similar impulses finally results in an automatic occurrence of the transmission, or, in other words, the action becomes habitual. Education consists largely in establishing such routes through the nervous tissue. Because of the greater plasticity of the neural mechanism in youth it is easier to open up and fix pathways of conduction than in later years. Moreover the earlier established lines of conduction become the more permanent.

The function of conscious control belongs primarily to the cerebral cortex. Here the sensory impulses and impressions are combined and elaborated into a controlling unity. Inasmuch as the interactions in the cortex are inconceivably complex and many of them are probably developed late in life—possibly as the result of individual experience—the cortex is a plastic organ which apparently serves as a seat for individually acquired correlations. According to Herrick there are more than nine billion cortical nerve cells at birth, a large number of which must develop further and make their connections. Presumably the various mental associations in the cortex are based on these connections and it is the large number of as yet unconnected synapses in the young human brain which make for flexibility and adjustment. It is thought indeed that never in any individual are all existing neurons developed, hence there always remains the possibility of making new associations. There seems to be some capacity for varying the connections of the dendritic processes even after they have once made connections. These neural changes occur in response to various external and internal conditions, and when it is realized that changes in consciousness accompany such changes, it is evident that the cortex possesses almost unlimited capacity for acquiring ideas and establishing new reaction patterns.

Characteristic Arrangements of Nerve Cells Are as Subject to Inheritance as Are Other Structures of the Body.—That the main features of the nervous system are inherited becomes obvious when we see that each kind of animal has its own distinctive numbers, arrangements and proportions of the various neural units. In man, for example, there are certain characteristics, types and groupings of nerve-cells which are reproduced generation after generation with remarkable fidelity. This means that in so far as these represent the mental make-up of the individual, his mentality is continuously linked with others which have gone before. The new-born child has all the nerve-cells in its brain that it will ever have but, as already noted, the ultimate linkages of the finer connectives between them, or at least the pathways of travel, remain in large measure to be made. At the age of seven the brain has reached practically its full size.

There is considerable neurological evidence to show that while the cerebral cortex is the seat of the chief intellectual reactions of man or at least of the highest of these, the machinery of the instincts and of the general emotional life is located in the sub-cortical material, or "old brain" as it is sometimes called. The "new brain" (cerebral cortex) does not occur in the animal kingdom until relatively late in evolutionary history, with the appearance of the amphibia. It attains to a rather meager development in the reptilia but with the advent of birds and mammals it comes more and more into prominence, although taking somewhat different courses of development in these two groups. The mammalian type has reached its supreme development in man, and so much of mental ability as is inherited probably resolves itself into inheritance of patterns of action in this cortical mechanism which render it easier for certain combinations than others to develop under ordinary conditions of environment, or in other words, which predispose us to a certain type of mental development.

Different Parts of the Cortex Yield Different Reactions.—The cerebral cortex, however, is not functionally homogeneous throughout. Certain regions have been shown to be motor, others sensory, and moreover, these regions are apparently further specialized so that a given one of them is associated with a specific type of sensory or motor response, not merely with responses in general. Thus by injuring one of the sensory areas we might destroy vision but not other sensations, or by stimulating one

of the motor centers we would get a response in a corresponding motor organ but not in all such organs. Likewise, it is probable that still different areas, the so-called "association areas," relatively of much greater development in man than in any other animal, are the regions in which various perceptions and conceptions are synthesized and formed into organized knowledge. Here also are engendered the volitions which when flashed through the motor centers become expressed in activity or behavior.

It seems highly probable that just as the sensory and motor areas differ in kind from one another, so we must suppose there are qualitative differences in various parts of the association areas so that the different parts give different reactions in consciousness; that is, each special mental ability of the individual is more or less centered in a special part of the cortex. And just as there may be variations in other structures of the organism so there may be variations in these areas. The "gifted" person in some one direction, whether it be in mathematics, music, painting, or what not, is on this hypothesis one who has that particular area of his brain which forms the basis for the talent in question more highly developed than it is in the average individual. And since such talents are handed down to descendants, this can only mean that a similar grouping of the neurons in the region in question has occurred.

Skill Acquired in One Special Branch of Learning Probably Not Transferred to Another Branch.—Such a differential arrangement of the brain-mechanism which presumably underlies the various mental abilities would lead to the inference that skill in one special branch of learning, in so far as it involves only certain centers of the cortex, would not be transferred to another branch based on different neural pathways and centers. Development of historical knowledge, for example, would not enhance one's mathematical ability, or vice versa. The testimony of various psychologists bears out this idea. In so far as certain factors of training, such as habits of industry, concentration, etc., are common to the study of either mathematics or history, the good effects of either discipline will probably be much the same, but the identity of effect vanishes as soon as the intrinsic characteristics of the subjects themselves are involved.

Just how far we are warranted, however, in carrying this idea of localized functions as regards the association areas is a

moot question. Our present attitude regarding the specificity of such localizations is largely a matter of inference based on analogy to conditions which obtain in other and better known parts of the brain, together with the indubitable differences in inborn abilities which exist between individuals. There is increasing evidence that the whole cortex operates more or less as a unit in all of the higher psychical activities.

Preponderance of Cortex in Highest Animals.—One of the most interesting conditions in the nervous system of the highest types of animals is the way in which the cortex has outrun the other parts of the brain in size and complexity and has come to dominate the organism more and more both directly and indirectly. Aside from the proportionately greater increase in size of the cortex, there is an abundance of anatomical evidence of this altered and probably altering system of control in man and the higher apes. This is well illustrated in the fiber tracts (nerve bundles) of the spinal cord.

More Long Fiber Tracts in the Spinal Cord of Man.—The spinal cord although having many nerve centers of its own is also in great part a large cable for conducting enormous numbers of fibers from one part of the cord to another, or to and from the brain. In man and the higher apes a considerably larger percentage of the total area of the cord is given up to the long fiber tracts from the brain to the body than in lower vertebrates. This progressive increase in long fiber tracts in the higher anthropoids probably marks more and more domination of the body by the higher brain centers and correspondingly less by the direct activity of the cord and by the lower brain centers. However, even in man, the simpler reflexes of the body still have their centers in the spinal cord.

Special Fiber Tracts in the Cord of Man and Higher Apes.—There are certain special tracts of the cord that are particularly interesting in connection with the increasing domination of the brain over the body, namely, the *pyramidal tracts*. These were the latest tracts to appear in the animal kingdom and are apparently the latest to become functional in the individual. It is believed that the development of the medullary substance (an enveloping sheath) of the common medullated nerve fiber marks the time of entrance of the fiber into activity and it is a significant fact that the formation of this sheath occurs last of all in the fibers of the pyramidal tracts, where it does not appear

till after birth. These tracts convey impulses from the brain to the body. They consist of two sets of tracts, in fact, one the crossed, the other the direct. As an anomaly, probably arising most frequently from instrumental injury at birth, the pyramidal tracts fail to develop normally, with the distressing result that the infant, although possessing perfectly normal brain activity and normal spinal cord reflexes, is unable to exercise voluntary control of the body. In other words the condition, like harelip, is one of suppressed development. At least this seems to be the most plausible explanation of what is known as *Little's disease*. Such unfortunates usually die early although they may survive for a few years.

The direct pyramidal tracts occur only in man and man-like apes. They vary considerably in extent in different individuals. They originate in nests of characteristic large cells located in the cerebral cortex and are regarded as paths, though not the only ones, through which volitional impulses are conveyed from the brain. They seem to control certain of the finer and more delicate movements of the body.

Greater Complexity in Associations and More Neurons in the Brain of Man Than of Other Animals.—It has already been noted that as animals stand higher in the scale of life while the general plan of their neural elements remain the same, there is increasing complexity in the number and connections of the neurons. The number of processes on individual nerve-cells is also greater. There is in fact much greater complexity in the number of processes and the inter-connections of the neural cells than in the numbers of the cells themselves. This would seem to indicate that the greater mental activities of higher animals depend more on richness in complex associations than on mere increase in number of neurons. The latter, however, is by no means unimportant as may be seen in man, for instance, in whom it is estimated that the cerebral cortex, that is, that part of his brain in which his more complex mental processes transpire, contains many millions more nerve cells than does the corresponding region of the brain of an anthropoid ape.

Of especial significance in the psychic make-up of man is his vastly increased capacity for inhibition. Although not possessed by all men in equal measure and not entirely wanting in lower animals it is a distinctive feature in all human conduct. Much of any child's education, particularly as it pertains to behavior,

must be concerned with training in the exercise of proper inhibitions. He must learn to suppress certain primitive types of reaction in favor of higher ones. This applies not only to motor activities but to trains of thought as well. The essence of self-control consists mainly in ability to substitute for one impulse or idea other compensating ones. And the secret of concentration lies in being able to banish irrelevant ideas and focus on the central thought.

The Nervous System in the Main Already Staged at the Time of Birth for the Part It Must Play.—It is clear from what is known of its anatomy that in the main the central nervous system is framed to respond in certain set ways, that there are determinative elements in it which control or determine the responses, and therefore the behavior of the body. The same evidence shows also, however, in the incompleteness of many of the associations, that while the stage is all set and some of the main features of the performance are determined at the time of birth, considerable yet remains to be done toward fitting the parts together and working up the detail. Just exactly what and how much is rigidly predetermined no one knows.

Human Conduct Determined by the Interaction of Inherited Neural Structures and of Individually Acquired Experiences.—When one considers the nature of mental attitudes, moral qualities, beliefs, or social traits, it is obvious that they are not inherited as such, but are the result of the interaction of inherent neural elements and such impinging factors as training, conventions, traditions and the like. Intelligence, in fact, seems to have arisen under stimulus of the environment and the consequent enforced recognition of it rather than as a mere efflorescence of the instincts. Those individual impressions which are stored away subject to recall as memory must plainly be individually acquired, or in other words, environmental in origin, and memories, of course, are highly important in determining later mental reactions. Thus human behavior becomes not only the expression of an inherited mechanism but also of the influence of the ideals, customs, traditions and conventions which come to bear upon the individual. These no less than the formal instincts and inherited inclinations determine the direction and outcome of an individual's reactions. Human social adjustments indeed are probably in the main learned adjustments and in so far as they are automatic should probably be reckoned as

habits rather than instincts. Nevertheless, since certain family strains acquire the same type of activity more readily than others there must be some inherent predisposing reason in the more favorable "set" of the underlying nervous mechanism of the more educable strains. The very capacity for forming habits is conditioned by heredity, as are the possible effects which may arise out of experience. Unquestionably temperament, personality and the like are the product of an inconceivably complex interaction of heredity and environment and no one has ever been able to determine the relative proportions of these respective influences.

In the light of modern psychology and psychiatry no one can doubt the influence of early environmental impressions on later behavior. Too many "inferiority complexes" with their accompanying sense of inability to cope with life have been traced to early fears or subjugations or thwartings, too many vagaries of mind and character have been found to originate in environmental maladjustments, to ignore the part played by environment on personality and conduct. And yet, here too, the probability of inherited trends in nervous make-up can not be ignored. Assuredly the brain is not a *tabula rasa* at birth upon which any record may be written. While adult characteristics are not predelineated in it, they are there as possibilities under certain conditions of environment. The possibilities of mental development are innumerable, hence untold numbers of hereditary potencies must remain unexpressed; the results of development can only be what some particular environment permits or calls forth. There is not the least doubt that many richly talented natures have never learned to use their endowment. This is the probable basis for whatever of truth there is in the maxim, "great crises always discover great men." On the other hand, under the fostering guidance of favorable training and influence even meagerly endowed minds may attain to reaches well beyond the average level of to-day.

Inasmuch as purely instinctive reactions can be modified or even replaced by acquired habits it is evident that mental and social environment contribute largely to the construction of the specific reactions, thoughts and ideals which determine human behavior. The neurologist Herrick, indeed, looks to the very conflict which must inevitably arise between inherent tendencies or instincts and individually acquired experience, as the source

of intelligence and voluntary control. Acquired elements in human conduct are possible because of this provision of intelligent adjustments in place of instinctive ones. As Paton expresses it "with the growth of the neopallium, the new brain, the coordination of conduct and the domination of instinct by intelligence were insured."

The Extent of the Zone That Can be Modified by Training Is Unknown.—There is little doubt that many of the paths of action are already firmly established. Others, although not irrevocably fixed, offer the least resistance and would "naturally" be taken if not counteracted or modified by the more or less artificial development and fixation of other paths through cultivation and habit. Yet others perhaps are largely neutral; they still await the initial decisive push which "choice" or external environment may mete out to them. As trainers of youth all that is left for us to do is to attempt to develop in certain ways the elements of this indefinite, impressible zone. Unfortunately, we must labor in the dark to a great extent as we have all too little indication of which the malleable factors of intellect and conduct are. We can only infer from long, intelligent and sympathetic observation of children in successive stages of their development. It is only by having clearly in mind the nature of our problem that our conclusions will finally come to be of enhanced practical value in the training of children. Observation to the present time clearly indicates that many children are strongly predisposed this way or that "as the sparks fly upward."

Various Possibilities of Reaction in the Child.—Despite the innate predeterminations of the tree, it is nevertheless our province to see that the twig *is* bent, but our work can only be done with due intelligence when we recognize something of the limitations of our material. Of the various possibilities of reaction we must see that certain desirable ones are realized, even, in some cases, if only to have others thereby excluded. It is a commonplace of psychology that all cerebral excitations, no matter what the origin, must vent themselves in some way and if this expression is not directed into proper channels it will very likely find improper ones. We must see that the young wearer of the coat of undetermined accomplishments gets it set by repeated performance into the habitual wrinkles of normal social conduct. For it is a trite observation that when habits are once well established it requires tremendous efforts to do otherwise than

as they dictate. There is not the least doubt that some of our subjects will respond much more readily to training in certain directions of habitual reactions than others, but we have always the consolatory knowledge that no matter how difficult the act may be at first, repetition reduces the difficulty.

While much of any youth's character must be determined by external forces brought to bear upon it, the ultimate climax of our effort and measure of our success will be the extent to which we have engendered in him the capacity for initiating and carrying out through his own volition those impulsions and inhibitions which tend to the highest good of humanity.

Training in Motive Necessary.—In the training of children, then, we must recognize first of all that there are decided inclinations or bents which, as long as they are not anti-social in nature, must be respected if not always encouraged. While it is necessary to utilize these as much as possible in their training still we must bear in mind that although it is natural for a child to follow certain interests, the fact remains that as regards social worth these natural interests may not be the most valuable. When this is true we must strive to develop others which will compel attention and thus become impelling factors in conduct. Where certain fundamental impulsions run contrary to the common welfare it is necessary to practise the child in the setting up of inhibitions or counter-impulses until this becomes habitual. He must be led to construct a protective mantle of appropriate scruples, doubts and fears. It is all important to get the proper motives for action to prevail in his mind.

Actual Practise in Carrying out Projects Is All Important.—But on the other hand it is equally important to see that the action is effectively carried out. In the matter of self-discipline, particularly, we may have many ideal impulses and realize that they should prevail over certain of our natural propensities, but unless we put forth effort to overcome the propensities our ideal impulses are of no avail. The world has many such moral paralytics to-day who can not "seize their languor as if it were a curling snake and cast it off." It is training in this very overcoming of reluctance, in this putting forth of actual effort toward worthy ends instead of merely memorizing precepts about the desirability of such accomplishments, that is so sadly lacking in our school and home life to-day. We prate of the importance of self-control, we say with our lips that the way to learn to

do is by doing, we proclaim that it is more vital to instil good mental and physical habits into our pupils than to stock them with information, we preach that mere fact training is as conducive to making a first-class rascal as an upright man, yet we jog on complacently in the well-beaten ruts of memory routine which require the memorizing of symbols rather than real understanding. We seldom require that our protégés make intelligent judgments based on evidence, we rarely exact of them decisions in matters of ethics, and almost never demand that they put their knowledge into efficient accomplishment. It can not be too strongly urged that we need less of formulæ learned by heart, less dead erudition pigeonholed in the brain like so many foreign bodies, and vastly more assimilation of knowledge into the living personality of the individual.

Where in school or home to-day do we find provision for such training? Our tendency is, in fact, just the opposite. According to the modern code, as it works out in many instances at least, the child must be taught through play. Though it is a truism that he who has not learned obedience can never be master of himself, the child of to-day must not be made to obey but be wheedled into changing his mind. If a given subject of study proves distasteful to him, the fault is the teacher's for not making it interesting, for he must always be led on by the thrill of fascination. In other words, the child must not only be allowed but be encouraged to take the path of least resistance. His own pleasure is to be the standard of his actions. Let no stern demands of duty interfere!

Is it any wonder that the products of such tutelage come into the activities of life self-indulgent and undisciplined, and although often recognizing our private and public shame in business, politics and conduct, still remain supine, evasive of the unpleasantness or hardships of reform, or inefficient or unwilling in accomplishing unselfish ends?

Interest and Difficulty Both Essential.—The writer does not wish to be understood as minimizing the importance of interest on the part of the child in what he is doing. Interest is undeniably the open sesame to desirable mental development; but what he does protest against is that not uncommon interpretation of interest which deems it necessary to eschew most serious consideration of a subject and evade such parts as present difficulties. Certainly if there is any fact that stands out prominently

in human experience it is the fact that nothing conduces to the development of moral stamina so much as the overcoming of difficulties, particularly distasteful difficulties.

Conduct Developed through Actual Performance.—Self-control and the will to do can be trained and crystallized into habit as well as can any other activity. It is a fact that one well grounded in morals by habit will successfully resist sub-conscious impulses to wrong-doing even when suggested in the hypnotic state. Conduct is largely a matter of growth through actual performance. For proper guidance of this growth there must, of course, be high ideals around which the feelings are led to cluster and by which they gradually come to be controlled.

Construction of Ideals.—The construction of such ideals through example, through precept, through appeal and through actual practise in self-denial and self-control on the part of the child, should be the foremost duty of the parent or teacher. Above all it should be remembered that imitation of teacher, of parents, of companions, is more of a factor than intellect in the moral action of children. At present educationally we are in a fever for vocational training for "practical" work, and in general for all things conducive to coaching our pupils in how to make a living, yet commendable as all this may be, is it not of even more fundamental importance to train them how to live?

The Realization of Certain Possibilities of the Germ Rather Than Others Is Subject to Control.—It may be said in a sense that there exists potentially in any germ all the things that can possibly come out of it under any obtainable conditions of environment. The very initiation of a given mode of expression by some environmental factor, however, often mutually excludes many of the others. We get a given average result ordinarily because development normally takes place in a given average environment.

As may be easily shown by experiment, this is manifest even in the instincts of lower animals. In the young the various instincts do not come into expression at the same time, and it not infrequently happens that if one of the earlier instincts becomes operative toward certain objects or situations, later instincts will have a wholly different relation toward these objects or situations than they would otherwise have had. As a result the whole life conduct of the animal is markedly modified. For example, many young animals immediately after birth have no instinct of fear. They do, however, have a strong instinct to

attach themselves to some moving thing and follow it. The utility of such an instinct, as for instance in the case of young chickens, is obvious. The object of attachment is usually the parent, but man may take the place of a parent and the young animal will fearlessly follow him about. However, if the young animal has had no experience with man during its earliest infancy a later instinct, that of fear or wildness, will have come into play and it will flee from him. It is clear, therefore, that by familiarizing the young animal with man before its instinct of fear has come to expression, certain habitual reactions are set up in it which inhibit or limit the application of its instinct of wildness as regards man. In other words, the whole course of its life has been altered by this simple experience. The same principle applies in even greater degree to the young of man.

We have seen in Chapter V that what in the ordinary course of nature was "predestined" to become one individual nevertheless contained the possibility of becoming four or more if the environing conditions were made such as to bring about a separation of the cleavage blastomeres. Or a fish egg that contained the possibility of becoming a normal two-eyed form also contained the possibility of becoming a one-eyed form and could be made to do so by certain unusual modifications of the conditions under which it develops. However, we must not be led so far by the plausibility of this comparison that we are misled, for the fact is that we are not creating anything new by these environmental upheavals, but are mainly altering features that already exist.

While development is a complex reaction between inherent organization and environment, for physical traits at least, organization is the predominant and more specific factor, environment the more permissive and directive factor. Even so, it is evident in such cases as the foregoing that what ordinarily are predestined ends can be altered by environment, and this is even more true of human social values since these are not so much absolute entities as attitudes toward an environment of changing things, events and people.

One of the chief objects of education is to train the young into those forms of behavior which will lead them to conform to the experience, traditions and ideals that the community, for the time being at least, accepts as necessary or desirable for its well-being. As has been seen, one does not inherit these extrinsic more or less shifting social objectives, but instead an inner neural

organization—so-called “action-patterns”—which through environmental influences including training, may be crystallized into habit-complexes adapted to social ends. Probably many of the inherent structures are relatively indifferent as regards such ends; the actual appearance of a particular trait is due merely to the fact that its development is possible under certain conditions of environment and that these conditions have prevailed in the given instance. In so far as there is an inborn trend in action-patterns ordinarily, it must be largely toward what is good for the individual, the community and the race; for any gross non-conformity to the demands of individual and racial hygiene in past generations has probably been weeded out by natural selection. Even where there is a specific bent toward antisocial conduct it may often be arrested through the awakening of a contrary impulse.

Our Duty to Afford the Opportunity and Provide the Proper Stimuli for the Development of Good Traits.—It is clearly our duty to see that the expression of good traits is made possible. We must throw a sheltering screen of social environment around the young individual which will fend off wrong forms of incitement and chances for harmful expression, and we must provide proper stimuli and afford opportunity for development of proper modes of expression. We must not forget that a normal instinct denied a legitimate outlet will not infrequently find an illegitimate one. Above all we must not forget the vital importance of establishing correct habits nor the possibility of even replacing undesirable ones by good ones. If training can redirect the machine-like behavior of as lowly a creature as the starfish into new courses, why should we be so willing as some of our geneticists would seem to be to throw up our hands and admit failure in the case of man before we have even made a rational attempt to correct the evils in question? Even in lowly organisms we have seen that behavior is not only the result of an innate constitution but also of the degree and kind of stimulations to which it has been subjected.

If the individual himself has not the initiative or will to make the attempt to set up proper or corrective habits, or to cultivate the necessary specific inhibitors, then all the more is it our duty to see that he is led by suggestion and drill into the proper routine of activities for their establishment. For if the individual with propensities toward moral obliquity is to be saved to society it must be through the stereotyping effects of good habits.

Heredity Not a Discouraging Fact.—In a letter which lies before me I find heredity designated as “an appalling, a discouraging fact, productive of a hopeless fatalism.” According to the writer it proclaims, “when you’re here you’re here, what you are you are, and that’s the end of it.” But is this true? Even ignoring the fact that it is through heredity that the hard-earned triumphs of the living organism are preserved and handed on to descendants, does not the solution of the adverse aspects of inheritance, as far as human values go, lie in making the right environment for *any* type of boy or girl, even the defective? The possibilities of different results from different trainings of the normal nervous system are probably almost infinite in number, and no one individual can attain to more than a small fraction of his potentialities, hence, the social and educational importance of seeing that the expression of “good” traits is made not only possible but likely.

Much of the protection of human society rests on the successful operation of an inhibitory mechanism by which instinctive or primal impulses may be suppressed or diverted into harmless channels. While children probably do not have these inhibitors at first, they have in general the capacity for acquiring them. Some, however, are so unfortunate as not to have the native capacity for developing the full complement of inhibitions and they are to that extent deficient. In spite of the best of training, they will react directly to the stimuli that fall upon them irrespective of whether the reaction is antisocial or not. These lacks vary in different individuals. In some only certain more or less specific inhibitions may be lacking and it is not uncommon therefore to find individuals who are socially valuable in some respects and untrustworthy in others.

Such inherent lacks as these, together with inborn suppressions or aberrance in the texture of the parts of the brain concerned with intelligence, make up the great bulk of “school failure,” that is based on heredity. However, it is obvious that one should not be too quick to classify a backward child as inherently defective. We well know that some organ-deficiency such as poor vision, poor hearing, a faulty stomach, thyroid-insufficiency, the presence of adenoids or the like may be an important contributing factor, although the element of heredity may also enter even here in that such physical impairments may be directly or indirectly of hereditary origin.

Mentality can be “normal” only when brain structure is normal,

and with any degree of innate brain deficiency there is a corresponding incapacity for education of the type planned for the normal child. In so far as deficient individuals have inherited their condition—and it is probable that inheritance is the most important factor in the feeble-minded, in affective deviates and in the genuinely stupid—heredity is of course an important factor in “school failure,” using failure in the sense of inability to attain to the standard set for normal children. However, even the feeble-minded of the higher grades at least, need not be complete failures if we will give them a training commensurate with their limited abilities and put them under proper supervision in an environment where the pressure is not too great and where they may have a sense of doing something worth while. Under such circumstances there is no reason why they should not lead reasonably happy and contented lives and be of some social value, or at least not a social menace.

Even though with our recently developed “intelligence tests” (page 357), we are not yet prepared to measure every particular tendency or trait of a child, we can at least appraise the main characteristics of body and mind and subject each individual to an environment which is favorable rather than hostile to his outstanding abilities. Unquestionably different varieties of human nature require different conditions for their most favorable development. A “superior opportunity” consists largely in being fortunate enough to be placed in that cultural sphere to which one’s native predispositions are adapted.

The great goal of society is to form a well-balanced, contented community in which the tremendously differentiated elements may each find congenial employment commensurate with its powers and its sense of the dignity and value of what it is doing, no matter how humble the task. Modern civilization is possible only with a mixed rather than a homogeneous population and there is a useful place in it somewhere for almost any conceivable type of reasonably normal human being, if the place and the person can be brought together.

Moral Responsibility.—Beyond question different men have different degrees of capacity for mental and moral training. All can not be held equally responsible ethically, but the lowermost limit of obligatory response to social and ethical demands necessary to rank one as within the pale of normal conduct is at such a level that any one not an actual defective can in a reasonably wholesome environment surmount it.

CHAPTER XIX

MENTAL AND NERVOUS DISORDERS

Some of the most important and serious problems which confront humanity to-day lie in the realm of mental and neural maladjustments. For human progress and social welfare are in last analysis based fundamentally on the results of normal reactions of human nervous systems. Any serious derangement of the latter may, and in certain cases must, lead to more or less disaster for the individual and disorder for society of which he is a unit. So appalling has the number of the mentally disordered become in modern times that the matter may well cause even the most thoughtless citizen to pause and consider.

Feeble-mindedness and Insanity Not the Same.—Specialists in mental disorders make a sharp distinction between insanities on the one hand and feeble-mindedness on the other. According to Goddard not only is there no close relationship between the two conditions, but in reality they stand at opposite sides of the psychical scale. In general, insanity is a degenerative process whereas feeble-mindedness (often also termed *amentia*) is an arrest of development. In the first case the victim loses part of the mentality he once had, in the second he stops short of normal development. What is commonly known as insanity is really a group of mental *diseases* of which psychiatrists recognize as many as twenty or more fairly distinct types; feeble-mindedness is a condition of mental deficiency, a lack of intellectual capacity.

The term "psychopathic personality" or "constitutional psychopathic inferiority," for want of a more specific name, is commonly used to designate a group of poorly balanced individuals who although not intellectually defective lack normal inhibitions and control; they are unstable, self-centered and sometimes sexually perverted. The antisocial type of these, unable to profit by reformative measures, are often referred to as "defective delinquents" and make up a considerable share of so-called "habitual criminals."

With the refinements of method which are being used in late

years in the study of the feeble-minded it has become evident that the individuals all classed together in past years as feeble-minded are really of several sorts. The mental defectiveness of one group in particular is found to lie not in lack of intellectual capacity but in aberrance of instinctive or emotional responses. Here belongs that not inconsiderable group of unstable, irresponsible mental defectives of fair or even occasionally excellent intelligence often described as uncontrollable or lacking in "moral sense." Since in psychological terminology an *affect* is the specific emotion or feeling aroused by a given stimulus, Professor Yerkes has designated this type of unfortunates as "affective deviates." Affective deviates are a fertile source of our juvenile delinquents, incorrigibles and criminals and therefore require very different treatment from that of the merely simple-minded.

The outside layer or "cortex" of the brain hemispheres is the region in which the more complicated intellectual and voluntary adjustments occur, but the "affective" centers concerned with emotion and feeling apparently lie lower, in the so-called "old brain," which from the standpoint of evolutionary history far antedates the cerebral cortex. The latter is first developed to any significant extent in the reptiles and only comes into prominence in birds and mammals. It finds its supreme expression in man. It is evident, therefore, that the mental defectiveness of affective deviates may be due to a deficiency in an entirely different part of the brain from that which is deficient in individuals characterized by intellectual incapacity and one can also see how such deviates may be intelligent and yet mentally defective.

Grades of Feeble-Mindedness.—As to the various grades of feeble-mindedness, while no sharp lines of demarcation can be drawn, a rough and ready test usually applied is the relative ability of such sub-normal individuals to take care of themselves. In all, the conditions exist from birth or shortly after. *Idiots* are such defective individuals as are unable to take care of themselves even to the matter of guarding against common physical dangers. Their mentality does not progress beyond that of a two-year-old child. *Imbeciles* can take care of themselves in the cruder physical ways, but are unable to earn their living. Their mental age ranges from three to seven years inclusive. *Morons*, or the "feeble-minded" in a more specific usage of the

term, can **under** proper direction become more or less self-supporting, but they are as a rule incapable of undertaking affairs which demand judgment or involve unrestricted competition with normal individuals. Their intelligence ranges with that of normal children from seven to twelve years of age. The last class grades up insensibly into the shiftless, ne'er-do-well types which exist in every community. It is the hordes of the feeble-minded in the restricted sense that afford our most serious problems to-day. The idiot and the imbecile are usually early and easily recognized and are kept more or less under restraint, but the higher grades of feeble-minded, the so-called moron type, can be detected often only by carefully devised tests.

The American Association for Study of the Feeble-Minded defines a *moron* as, "a mentally defective person having a mental age between 84 months and 144 months, inclusive, or, if a child, an *intelligence quotient* between 50 and 74." The intelligence quotient, commonly designated I. Q., is determined by dividing the mental age as found through a standardized series of tests, by the actual age of the individual. Thus if a child of 12 showed a mental age of a 9-year-old his I. Q. would be $9/12$ or (thrown into the form of a whole number) 75, while if a child of 9 showed a mental age of 12 his I. Q. would be rated at $12/9$ or 133. The Binet scale or some of the numerous modifications of it is the standard commonly used. It is reliable in determining mental defect below a mental age of ten or ten and a half years in individuals whose actual age is fifteen years or over, but for borderland types much additional data—physical, mental and social—is necessary for accurate diagnosis. Over 80 per cent. of the feeble-minded fall in the class of morons.

Epilepsy.—Epilepsy is a chronic functional disease characterized by "fits" or convulsive attacks in which generally there is loss of consciousness. Ordinarily the attacks last from five to twenty minutes. They vary greatly in frequency and in severity. The severe form is termed *grand mal*, while the mild form in which dizziness or related sensations occur instead of convulsions and loss of consciousness is called *petit mal*.

Although epileptics are not classed as imbeciles ordinarily, as a matter of fact no sharp distinction can be drawn between the two classes. Doctor Wilmarth, for many years superintendent of the Wisconsin Home for Feeble-Minded, says, "Epilepsy and mental deficiency are as closely related as branches on the same

tree. . . . Over one-half and perhaps two-thirds of all feeble-minded are subject to convulsive seizures at some period of their lives, and we are never surprised at the appearance of epilepsy in any feeble-minded person. On the other hand, so small a percentage of epileptics maintain normal mental actions as hardly to be worth consideration . . . even those who retain a normal mind in the early stages of the disease almost infallibly become imperfect later." How slight a chance the epileptic has of ever becoming normal may be inferred from a statement made by Doctor Frank Billings in a paper read before the Illinois State Medical Society in 1909 to the effect that "ten per cent. or more can be cured by proper care." From its opening in 1896 to 1918, a period of twenty-two years, the Craig Colony of New York had pronounced recovered only 62 out of 4,077 epileptic patients under treatment.

Prevalence of Insanity, Feeble-mindedness and Epilepsy.—

There is no way of determining accurately the prevalence of mental and neural diseases and defects in the United States because no one knows how many such unfortunates there are outside of institutions. There are some 700 public and private institutions in the United States which care for patients with mental disease, mental defect or epilepsy. The forthcoming report of the Federal Census Bureau lists altogether 526 hospitals for mental disease and 154 institutions for feeble-minded and epileptics.

In 1923 there were some 285,500 patients in hospitals for mental disease, nearly 2,000 in psychopathic wards in general hospitals and 22,839 such patients on parole. How many there were out of contact with hospitals there is no way of knowing. According to estimates based on statistics of the New York State Hospital Commission approximately 1 out of 25 persons becomes insane at some period of life. There are more persons in our hospitals and homes for mental diseases and mental deficiency than there are students (726,124 in 1926) in our colleges and universities. In 1924 some 76,000 persons were graduated from our colleges and universities while there were about 75,000 first admissions and 16,000 readmissions to our hospitals for the insane. According to a note in the Mental Hygiene Bulletin there are approximately 24,000,000 individuals in the United States attending public and private schools and colleges, about 4 per cent. of whom, or 960,000 will at some period of

their lives enter a hospital for mental disease if the present rates for first admissions to such hospitals continue. According to Prescott F. Hall the average life of an insane patient is 12 years.

The rate per 100,000 of population of patients with mental disease under institutional treatment increased from 118.2 in 1890 to 220.1 in 1920. In New York State in 1925 the rate of admissions per 100,000 of population was 416.7. Such figures of course do not indicate a correspondingly rapid increase in insanity but rather the greater accuracy of recent enumerations, the growing practise of sending the insane to hospitals, and to some extent, reduction in their death-rate. Whether or not mental disorders are increasing in greater proportion than general population we have little reliable data from which to form an opinion. Regarding insanities we are almost wholly in the dark; many alienists believe that there has been an actual relative increase in recent years. Concerning epilepsy and particularly feeble-mindedness there is evidence of a disproportionate increase to general population, but only scattering studies have been made and statistics for comprehensive conclusions are not available. According to Davenport and Weeks, in the State of New Jersey the number of epileptics doubles every thirty years and from a survey of a number of counties in Pennsylvania made by Dr. Key one learns that not only was the birth-rate among feeble-minded mothers more than twice that of normal mothers but the survival rate of the young of such defective mothers was also more than twice that of normal mothers. Reports from England are in agreement that in spite of the Mental Deficiency Act which has been in force for ten years, there is still an increase in feeble-mindedness.

There is greater difficulty in estimating the total number of feeble-minded than of the insane because only a small proportion of mental defectives are cared for in institutions. Laughlin estimates that only about 5 per cent. of the feeble-minded needing custodial care are actually receiving it in institutions. It is generally conceded that less than 10 per cent. of the feeble-minded are cared for in institutions. With the refinements of methods by which the feeble-minded may be diagnosed increasing numbers are coming to light. The number recorded depends largely on where we set the border-line of mental deficiency. As a matter of fact there is no clearly cut border-line since feeble-

mindedness grades over imperceptibly into low mentality. Most of the discrepancies in estimates of numbers are due to our uncertainty about the borderland types. Thus one finds estimates for the United States ranging all the way from 400,000 to 2,000,000 or even 4,000,000. The total number of mental defectives in institutions in the United States on January 1, 1920, was 40,519 and if this represents 10 per cent. of the clearly feeble-minded—a not uncommon estimate—then something between 400,000 and 500,000 is probably a minimal figure for the present time. On the basis of Dr. Laughlin's five per cent. estimate the number would stand somewhere between 800,000 and 1,000,000. When Massachusetts had a population of 3,500,000 Dr. Fernald estimated that there were 60,000 intellectually sub-normal persons in the state. If the same proportions hold in other states this would give an estimate of 1,800,000 for the United States. On the other hand, the recent report of the Wisconsin Mental Deficiency Survey conducted under the auspices of the National Committee for Mental Hygiene and a special state committee reveals conditions which are probably more nearly typical for most states. The total population of Wisconsin is about 2,700,000. A careful study was made of the various state and county penal and charitable institutions, and of 8,000 representative school children. According to the estimate in this report, there are in all 18,000 feeble-minded individuals in the state. This is 2,000 more than the estimate from the army count made during the war. Of these, only 1,126 are in the two state institutions, and 433 others in special classes in the schools. On the general estimate that there are one-third as many insane as feeble-minded, the number of insane in the state is recorded as about 6,000. Of the approximately 400,000 school children in the grades of the public schools, it is estimated that 40,000 are so handicapped mentally as to be unable to compete on equal terms with their fellows. Of these, 2,800 are classified as actually feeble-minded, but if we add the border-line cases, the total rises to 7,200. Approximately 800 children in the public schools of the state are afflicted with epilepsy and 1,200 are classed as of psychopathic personality; that is, they are neither feeble-minded nor insane, but are characterized by frequent behavior difficulties. This record of mental ills is surely enough to give any state cause for serious thought.

It should be borne in mind that the Wisconsin estimates are

the result of a careful special survey and are not mere guesses. If they represent average conditions in the United States, as they probably do, then our total number of feeble-minded would be something over 700,000.

According to the Federal Census Bureau, in 1923 there were 23,760 epileptics in almshouses and institutions for the care of feeble-minded, epileptics and insane, but since only a small percentage of epileptics are in institutions this tells us little of the total number. A rather common opinion among experienced investigators in various states is that there is about one epileptic to each 350 to 500 inhabitants. This would give a total of between 200,000 and 300,000 for the United States.

Imperfect Adjustments of the Brain Mechanism Often Inheritable.—The brain mechanism is as much a product of ancestry as is any other structure of the body, and it is obvious therefore that imperfect adjustments of its structure must be as subject to the laws of inheritance as are other malformations of the body. Because of the extreme complexity and delicacy of its mechanism, it is peculiarly liable to derangements which even when slight, may have far-reaching effects. And just as with other defects, mental disorders may thus flow from pre-existing ancestral maladjustment of the nervous system or of some structure affecting it, or they may be caused by environmental influences such as syphilis, alcoholism, degeneration of the blood-vessels and injuries.

It may be thought that few insane and mental defectives are married, but a glance at available statistics shows this opinion to be erroneous. The annual or biennial reports of state institutions for the insane show that considerably over half the patients are married or have been married and there is no reason to believe that conditions are different in private institutions. For example, of 443 first admissions to the Wisconsin State Hospital for the Insane in 1923, 192 of the patients were single, 193 married, 57 had been married and the status of one was unascertained; and in 1924, of 482 first admissions, 212 of the patients were single, 211 married, 52 had been married and the status of 7 was unknown.

One of the most disquieting facts in the situation in most states is that constantly many patients are on parole subject to recall. This means that although it is recognized that these patients are likely to have to be returned to the asylum or hospital, little

or no restraint in the meantime is placed on their marital relations. Is it any wonder under the circumstances that we find Doctor Charles Gorst, one time superintendent at the Mendota Hospital, voicing in a report the following vigorous protest:

"No one doubts for a moment that defective mental conditions are transmitted from parent to child as surely as physical defects and deformities. Every one knows that it is common for defectives to be attracted to each other and marry, and that the defects of both parents are liable to be transmitted to the children. It is also true that there are more children born in such families; and for that reason the percentage of defectives is continually on the increase. The report of the state of Illinois shows the increase to be alarming, and many other states are no better. It is absolutely wicked that the persons suffering from periodical insanity should be allowed to return to their homes to propagate and scatter their children about the state as dependents."

As to the feeble-minded the universal tendency is for defective to mate with defective. Davenport gives a list of examples beginning with such a one as this: "A feeble-minded man of thirty-eight has a delicate wife who in twenty years has borne him nineteen defective children," and similar instances will be found recorded with appalling frequency in the numerous surveys and reports which have been made in various states during recent years. Marriage, furthermore, is a negligible incident to many of the feeble-minded for they frequently have illegitimate children.

A Neuropathic Constitution May Express Itself Differently under Different Conditions.—Some of the difficulties in getting genealogies of specific forms of insanity are obvious from the following quotations chosen from the works of eminent psychiatrists. Kraepelin, for instance, expresses the opinion that: "The psychopathic charge of a family may reveal itself not only by the appearance of mental disorders but also by other forms of manifestation. Here belong before all, those diverse slighter deviations from mental health which go to make up the borderland of insanity: nervousness, states of anxiety and compulsion, constitutional depressions, slight hysterical disorders and forms of feeble-mindedness, tics; also odd characters, peculiarities in mode of living, criminal tendencies, lack of self-control,

intemperance, love of adventure, mendacity, suicide on an inner basis."

From the volume of Church and Peterson on *Nervous and Mental Diseases* a further confirmatory opinion may be cited: "In determining the factor of heredity we must not be content with ascertaining the existence of psychoses in the ascendants, but must seek, by careful interrogation of various members of the family, for some of the hereditary equivalents, such as epilepsy, chorea, hysteria, neurasthenia, somnambulism, migraine, organic diseases of the central nervous system, criminal tendencies, eccentricities of character, drunkenness, etc., for these equivalents are interchangeable from one generation to another, and are simply evidence of instability of the nervous system. It is the unstable nervous organization that is inherited, not a particular neurosis or psychosis, and it must be our aim in the investigation of the progenitors to discover the evidence of this."

Many Types of Insanity.—The commonest manifestations of insanity are undue depression, apathy, excitement, instability, obsessions, hallucinations and delusions. Some mental disorders are associated with recognizable structural changes in the nervous system, but the structural basis of many is not known.

In general there is more doubt about the inheritability of some of the insanities than about cases of mental deficiency. The term insanity is merely a loose descriptive one, and we shall gain little definite knowledge about the inheritance of such maladies until we study each separate insane diathesis specifically. Psychiatrists recognize many different forms of insanity, some of them very distinct from others and the product of unrelated underlying causes. Often it is only a question of degree or sometimes a matter of chance as to whether a given individual is certified as insane or not. A mentally unbalanced person who manifests certain antisocial activities is sure to be classed as insane, whereas another individual with the same predisposition in a less degree might pass unrecognized. It is almost impossible in some instances to tell just where the border-line between an abnormal and a normal constitution lies. Many of the idiosyncrasies of the insane, indeed, are merely exaggerations of characteristics seen in normal people. Recent studies of the psychology of the insane show that most of their hallucinations and delusions are closely related to some previous mental experience they had before becoming insane. And it has been found that the surest

means toward removing the obsessions of the patient in curable cases is to ferret out these earlier experiences and correct the wrong impressions regarding them. Again, certain forms of insanity do not become manifest except as special reactions to particular environmental conditions, and if these conditions do not happen to occur, then the neuropathic constitution, though existing, would not be revealed. Certain critical periods of life such as puberty, pregnancy and the close of sexual life are particularly likely to test out the mentally unstable, although such individuals may have maintained normal mental balance up to the crisis in question.

Insanities Not All of the Same Genetical Significance.—Of the various kinds of insanity some seem to be of much greater genetical significance than others, not only because they are strongly heritable, but also because of the periodicity of the attacks. The patient may be repeatedly in and out of the asylum and in his sane intervals wholly unrestrained as far as propagating his kind is concerned. *Manic depressive* psychoses and *dementia præcox* (adolescent insanity) represent by far the largest number of admissions to general hospitals for the insane, and both of these very frequently have a hereditary basis.

Fig. 90, a chart showing the insanity in a local family as worked out by one of my students, is a good example of a recurrent type. The father (Fig. 90, p. 343) was about eighty-two years old when the record was made. His memory was poor and he could not talk connectedly, although this was possibly attributable to old age rather than to insanity. His brother, written to in Ireland, stated that to his knowledge there had never been insanity in his side of the family. The mother (2) was insane at nine, again at twenty-nine and again at thirty-six. In her later life she has been in the Mendota Hospital for the Insane five times and in the County Asylum twice. The eldest daughter (3) has been in the State Asylum five times and is now at home. The next daughter (4) spent five months in the asylum in 1885. Another daughter (5) likewise spent a short period in the asylum. Two sons (6, 7) have each spent two periods in the asylum, and a third son (8) has had an attack of insanity. The youngest child died at the age of three. Thus of eight adult children six have been insane at some time. The cases in this family seem all to be instances of manic-depressive insanity.

Certain Forms of Insanity, But Not All, Seem to Behave as Mendelian Recessives.—A number of psychiatrists and investigators of the inheritance of insanities (Rudin, Lunborg, Davenport, Rosanoff, Jolly), although working independently and in different countries, concur in the opinion that manic-depressive insanity, dementia præcox and allied psychopathic conditions tend to occur after the manner of a Mendelian recessive. Questions of degree, of incomplete or irregular dominance and probably of multiple or modifying factors enter to complicate matters. Confusion may also arise from the fact that probably people of the same underlying neuropathic or psychopathic inheritance may differ widely in their symptoms. No wholly satisfactory classification of the varied forms of insanity has yet been attained. Again environmentally-caused insanities may

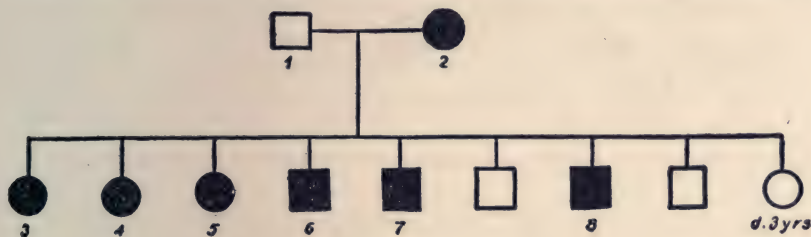


FIG. 90

Inheritance of insanity in the L— family. See text for description.

be intermingled with hereditary types in some records of family strains showing mental disorders. Furthermore, individuals who have not yet reached middle age, listed in family histories as normal may not be so since most of the insanities usually appear rather late in life. On the other hand *Huntington's chorea* (an affliction of adults characterized by irregular movements, speech disturbances and dementia) is transmitted as a dominant, and in all probability at least half of the offspring of an afflicted individual will inherit and manifest the defect. As to inheritance of various other psychoses we have too few accurately charted pedigrees for most types to make very positive statements about their degree or manner of inheritance. Little can be said beyond the statement that there is a decided tendency for various forms to recur in offspring.

There is abundant evidence that mental disorders occur more

frequently in some family stocks than in others, and various alienists have noted a decided tendency for the same types of psychoses to reappear in the same strain, but the inheritance is apparently so complicated that it can not be reduced to a simple unit character basis. Dr. Schuster, for example, from a statistical investigation of the London County Asylums finds a marked tendency for delusional insanity to run in families and a strong correlation between members of the same co-fraternity in cases of dementia præcox and of the periodically insane. Strohmayr, a German investigator, records manic-depressive insanity as frequently reappearing in the same form. Heron, from records compiled over a long period of time by Dr. Urquhart, Superintendent of a Scottish asylum, and also from extensive data collected by Pearson, concludes that insanity is inherited to about the same extent as intelligence, stature and various other traits. He believes that his results indicate "that if *completed* histories are taken 40 per cent. of insane offspring of insane parents is not an overestimate, and that in this memoir we have erred on the side of lessening the intensity of inheritance in taking 25 per cent. of the offspring of insane persons to be insane."

Where more than one case of insanity occurs in a given family or stock it is presumptive evidence that a hereditary defect is at the bottom of it. As Dr. Wilmarth says, "Mental accident may occur in any family, but it is rarely a second case occurs unless there is a tendency to nerve degeneracy." For example, of 818 insane in the Wisconsin State Hospital for the Insane during the biennium 1909-10, 187, or practically one-fourth, were positively known to have insane relatives. Of these, 24 had insane fathers, 31, insane mothers, 30, insane brothers, 23, insane sisters, 25, insane uncles, 21, insane aunts, and 21, insane cousins. Where definite information could be obtained it was found that of the 5,700 admissions of insane patients to the New York state hospitals during the year ending September 30, 1911, 27.7 per cent. of the cases showed a history of insanity in the family and an additional 22.9 per cent. showed a history of alcoholism, nervous diseases and the like.

From the report (1915) of a commission appointed by the legislature to investigate the extent of feeble-mindedness, epilepsy, insanity and other conditions of mental defectiveness in Michigan one learns that among 4,917 insane individuals concerning

whom satisfactory information was obtained, 65.4 per cent. "had among their ancestors or family such hereditary influence as insanity, apoplexy or paralysis, psychopathic abnormalities or alcoholism."

Some Insanities Not of Hereditary Origin.—On the other hand in many cases of insanity there is no discoverable hereditary basis. Some alienists believe that self-poisoning known as *auto-intoxication*, due to improper elimination of poisons generated through faulty digestion or metabolism, if of long standing, may be not only a contributory but a more or less direct cause of insanity. About 20 per cent. of insanities of men living in cities and about 15 per cent. of those living in the country seem to be directly related to the intemperate use of alcohol. The corresponding figures for women are 7 per cent. and 1 per cent. respectively. Constitutional neural instability, however, probably underlies most alcoholism. General paresis or softening of the brain is caused by syphilis. About 22.5 per cent. of the first admissions to hospitals for the insane from city-dwelling men, and 8 per cent. from men living in the country in the state of New York are cases of this kind of insanity. The corresponding figures for women are 5.5 per cent. and 2.5 per cent. respectively.

Some psychiatrists are inclined to attribute much insanity to focal infections instead of a hereditary predisposition although before their opinions carry full conviction they will have to explain why it is that such infections produce insanity in certain individuals and not in others who may be equally or more highly infected. The indication would seem to be that a constitutional instability is involved in the case of the former which is lacking in the latter.

In our present state of knowledge—or lack of knowledge—we are probably not justified in attributing at most more than 50 per cent. of mental diseases directly or indirectly to inheritance. Even in the inherited forms environment unquestionably plays an important part in the expression of the malady. As a practical matter the hopeful fact should not be lost sight of that individuals with an unfavorable lineage may often, in the light of the new science of mental hygiene, do much to overcome constitutional tendencies by learning to avoid adverse influences and to make proper social adjustments. Such persons, however, should give serious thought to the matter before bringing children into the world.

Increase of Public Interest in Feeble-mindedness.—During the last fifteen years there has been a rapidly increasing recognition of the fact that feeble-mindedness enters into and complicates many social problems, particularly those of delinquency, crime and pauperism. Even many of our cross-currented legislative bodies, through pressure of the inescapable facts, have been stirred into uneasiness to the point of instituting surveys with the aid of suitable state or national organizations. Notwithstanding the unexpectedly serious conditions revealed by such surveys, surprisingly little has been done by later legislatures to remedy the situation. This is due probably to the shifting personnel of such bodies and the new issues which are constantly arising rather than to any lack of good intentions. If valuable efforts are not to be wasted and constructive policies are to be instituted, however, some sort of follow-up system should be devised.

Examples of Hereditary Feeble-mindedness.—No one can look at the remarkable series of charts and records brought together by Doctor Goddard of the institution at Vineland, New Jersey, and by other directors of similar institutions, and doubt for an instant the inheritability of feeble-mindedness and allied defects. In some instances the family history has been followed back as far as five generations, and it is always the same dire sequence of insanity, idiocy, epilepsy or feeble-mindedness, from generation to generation. For example, Fig. 91, p. 347, is one of Doctor Goddard's charts. It shows thirteen descendants of a supposedly normal father (possibly a carrier) and a feeble-minded mother, of whom seven were feeble-minded, the others dying in infancy. The mother herself was one of seven feeble-minded children, who were in turn the descendants of feeble-minded parents, of whom the woman had five feeble-minded brothers and sisters. In Fig. 92, p. 348, he shows mental defects running through four generations. Fig. 93, p. 349, is a remarkable exhibit which, starting in the fifth generation back with a feeble-minded, alcoholic man—the mental condition of his wife being unknown—shows that in every generation down to and including the present there has been nothing but feeble-minded (or worse) offspring, leaving out of account two unknown and a number who died in infancy without revealing their mental condition. This is true notwithstanding the fact that in the course of the various generations there had been several matings

with apparently normal individuals. The new blood, however, instead of redeeming the tainted stock, itself became vitiated. The numerous specific cases of inheritance of family traits reviewed in recent books or in special reports of trained workers give us abundant confirmatory evidence of the inevitable inheritance of various nervous and mental defects.

Difficult to Secure Accurate Data.—It is obvious, of course, that in tabulations such as these there may lurk considerable margins of error. Notwithstanding our Binet-Simon and other tests for feeble-mindedness, for example, there is yet much to be desired in the way of accuracy. Many cases just bordering normality are by no means easy to decide. Then again in most human records, when one gets back beyond the third or, at most, the fourth generation, the investigator has to depend on the

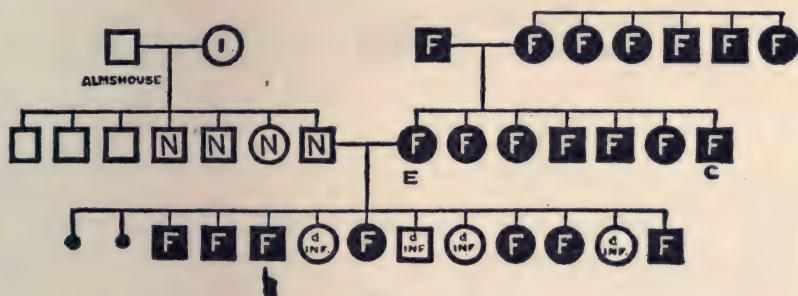


FIG. 91

Inheritance of feeble-mindedness (after Goddard); squares represent males, circles, females; F, feeble-minded; N, normal; E, epileptic; I, insane; C, criminal; T, tuberculous; d, inf., died in infancy; the hand shows the individual from whom the record was traced back; small black circle indicates miscarriage.

hearsay evidence of relatives, friends or neighbors, and how vague this generally is can only be appreciated by those who have themselves tried to collect such data. But in spite of all the difficulties, there is little doubt that the more carefully prepared records are sufficiently accurate to establish the fact beyond dispute that defective tends in large measure to breed defective.

One serious drawback in making a study of the inheritability of insanity and other nervous disorders is that so far we have dealt mainly with mass effects rather than specific neuroses. But even when the latter is attempted we are confronted by the fact that there are various intergradations of the recognized

80 apparently normal, who are nevertheless hopeless slaves of a neurotic heredity, direct or collateral.

"In a study of 15 imbecile girls, 3 were recognized prostitutes, 9 had each 1 illegitimate child (2 being the result of incestuous intercourse with brothers); 1 had 2; 2 epileptics had, the one 3, and the other 4 idiot children.

"Four feeble-minded women had 40 illegitimate children.

"A feeble-minded woman living in an almshouse since early childhood, allowed to go out to service periodically, had given birth to six illegitimate children, all inheriting her defect.

"An imbecile drunkard is the father of three feeble-minded children. The daughter, seduced before the age of sixteen, gave birth to an idiot child; one son is a harmless imbecile, but the other is a moral imbecile, a sexual pervert, a thief on the streets, and a pyromaniac, firing in sheer wantonness a large mill property.

"Another shows the entire family for three generations below normal. Father, mother, mother's sister, and father's uncle, all

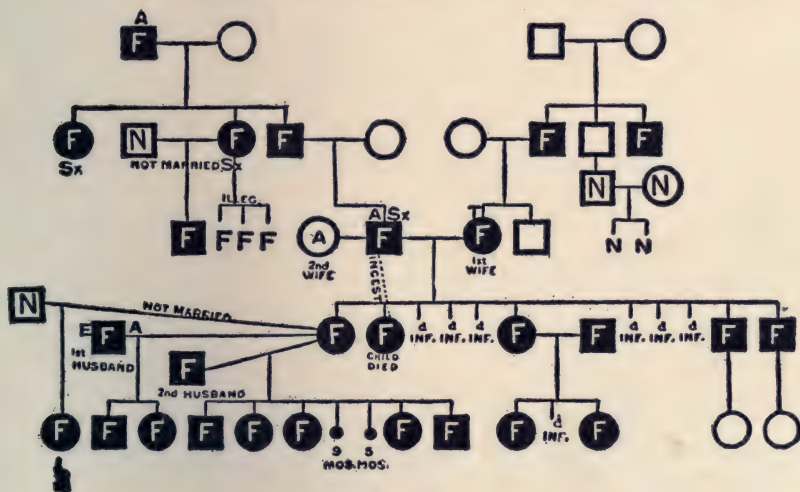


FIG. 93

Inheritance of feeble-mindedness (after Goddard); symbols same as in Fig. 91, p. 347.

imbecile. Five children feeble-minded. One girl had a proposal of marriage, and one boy is married to a feeble-minded girl.

"One insane woman, whose brother and sister committed suicide, had five sons. The oldest, feeble-minded, a drunkard and hobo, had one son, a criminal. The second son, insane, had three

imbecile children. The third, an insane epileptic, had three imbecile sons, one of whom was an epileptic. The fourth son was insane. The fifth, apparently normal, had a morally imbecile son and an epileptic daughter."

Yet, striking as is the evil outcome of such conditions, Doctor Barr points out that in Pennsylvania only a small percentage of the feeble-minded are sequestered. Most of such irresponsible individuals are left to work havoc in society by producing their kind. The same note of warning is sounded in all of the reports of the numerous surveys and investigations which have appeared steadily during the past fifteen years. From the 1920 report of the Wisconsin Mental Deficiency Survey, for example, one gains some very instructive information:

"We do not believe Wisconsin's state and county institutions are any longer acting as lying-in hospitals for the reproduction of these defective and unfit strains. We do believe and know, however, that in nearly every community of the state there are feeble-minded stocks that, nurtured and cared for by the church organizations, relief agencies, and good people of the community, protected from the hardships and vicissitudes of life, are thus encouraged to leave behind them defective children, who in turn furnish their quota to the state and county institutions of Wisconsin. . . . It can be clearly shown that mental defectives for the most part, if untrained and unsupervised, are dependents or delinquents. They neither starve nor go without clothes or shelter, but are maintained at the expense of others, and are dependent on the public purse. They receive support from overseers of the poor, organized charities, neighbors, friends, relatives, churches, from strangers by begging, and from various sources. . . . But the fact is that proper institutional provision, segregation and supervision of such cases is not an added expense to the commonwealth, but a better organized, more economical way of bearing an already existing burden, and a more equitable distribution of it. . . . In reckoning up the expense of these individuals, have we considered the loss that results from spreading venereal infection, and the expense involved in providing clinics for the treatment of this condition? Have we considered the losses entailed upon theft, burglary, incendiarism, assault, murder, and the many other antisocial tendencies of the feeble-minded, together with the cost of apprehension, detention, conviction, and maintenance in state and county institutions?"

Inheritance Not a Factor in Some Cases of Mental Deficiency.—On the other hand as our data show, there remain about one-third of the mentally deficient type to be accounted for on other than a basis of heredity. As already noted, some of these are doubtless the product of suppressions of normal development by various extraneous factors operating before or shortly after birth. There is one class particularly, estimated by some authorities as constituting as high as thirty per cent. of the feeble-minded, which is unusually puzzling. These are the so-called Mongolians. The name is given because the features of such individuals bear more or less resemblance to those of some of the Mongolian races. The defect does not seem to be hereditary although it is usually congenital. It appears to be due to something which interferes with prenatal development. Whatever the conditions, whether lack of nutrition in the mother, endocrine disturbance, alcoholic or other poisoning, the cases seem to be as hopelessly incurable as are the hereditary forms. From the social standpoint, of course, such individuals are in their immediate generation, as incompetent or as dangerous to society as those suffering from the more surely known hereditary forms of mental defect.

There is a tendency on the part of certain clinicians to reduce the estimates of hereditary feeble-mindedness and to attribute proportionately more influence to such factors as adverse prenatal conditions, the lack of some endocrine secretion, birth injuries and certain infectious diseases. There can be no doubt that in many cases the cause is obscure or ambiguous. Feeble-mindedness may result from a variety of factors either environmental or hereditary and there is no reason to doubt that adverse environment not infrequently germinates the seeds of hereditary disorders which would otherwise remain dormant. Wallin, who has given much time to the study of mentally deficient children, impressed by the ease with which defects and monstrosities (Chapter V) in embryos or fetal young can be produced by various toxic substances operating directly on the germ-cells or through the soma of the mother, believes, "that many destructive agencies, especially toxins, may injure the germ-plasm, or the brain of the embryo or the fetus, or the brain of the young child" and he is inclined to look to such blastophthoric agents as the source of much feeble-mindedness.

Inherited Conditions of Feeble-mindedness and Epilepsy

Tend to be Recessive to Normal Conditions.—As to the mode of inheritance of the various forms of feeble-mindedness, the evidence points to such defects in the main as being recessive. However, no particular grade can be picked out and shown to be a pure recessive. For instance, the children of two epileptics will be defective but it is impossible to predict always whether the defect will appear as epilepsy or feeble-mindedness. This is doubtless due to the fact that mental deficiencies even of the inheritable type are not all due to the same specific cause, and in many cases the individual is defective in more than one direction. If one or more of a great number of units which are necessary for complete mental development are lacking, obviously mental deficiency will result. In other words, feeble-mindedness and allied disorders may not be definite characters, but simply evidences of the fact that the nervous system has not developed all factors necessary for normal mental coordination. Goddard, however, one of our best authorities on the heredity of feeble-mindedness, is inclined to regard the condition as a unit character, "due either to the presence of something which acts as an inhibitor, or due to the absence of some stimulus which sends the normal brain on to further development."

Supposing nervous defects finding expression in feeble-mindedness, epilepsy and related conditions, to act as a Mendelian recessive, then the marriage of one such defective with another should yield only mentally enfeebled offspring. How nearly this expectation may be realized is seen from the following examples.

In an extensive study* of feeble-mindedness, Doctor Goddard points out that of 482 children with both parents feeble-minded all but six were feeble-minded. Even the exceptions may be apparent rather than real as there is possibility of mistake in judging the condition of the parents or of the children themselves. Moreover, with the feeble-minded one is not always sure of the paternity of a child, as is instanced by Doctor Goddard in a case quoted from Doctor Emerick in which of twelve children in a white family with both father and mother feeble-minded ten were feeble-minded and two were not, but these two were *mulatto* children.

In a paper by Weeks (*The Inheritance of Epilepsy*), in part an extension of an earlier joint paper by Davenport and Weeks,

* *Feeble-mindedness; Its Causes and Consequences*, by Henry H. Goddard, The Macmillan Company, 1914.

is recorded among others a study of 27 fraternities in which both parents were either epileptic or feeble-minded. Of the 28 progeny, 19 lived long enough to reveal their mental state. Of these 3 were feeble-minded, 8 epileptic and 8, from parents who developed epilepsy late in life, were what Doctor Weeks terms "tainted." In 15 fraternities in which one parent was epileptic and the other feeble-minded he found there had been 81 conceptions. Of these 7 were too young to classify and 19 had died before fourteen years of age. Of the remaining 55, 28 were epileptic, 26 feeble-minded, and 1 insane. Again, in 9 families in which the parents were both feeble-minded, of the 38 surviving offspring who were old enough to classify, 7 were epileptic, 29 feeble-minded, and 2 drunkards. In 5 families where one parent was insane and the other epileptic or feeble-minded, 5 children died before the age of fourteen, the condition of 2 was unknown, 2 were epileptic, 4 feeble-minded, 1 insane, 8 tainted, and 7 seemingly normal. Regarding the latter Doctor Weeks says they came from two families where in the one case the father's insanity seemed to be traumatic and in the other alcoholic.

In a few cases where the defect in one parent has apparently been of a type different from the defect of the other parent a "normal" child was produced. That is, disregarding the possibility of illegitimacy, presumably each parent carried normality in the trait defective in the other so that the child became simplex with reference to each defect. Davenport points out that not infrequently two deaf-mutes whose defects are due to different causes may have normal children.

In general, however, the reasonable expectation is that where two feeble-minded individuals marry, a very common occurrence, the children will all show mental deficiency. A mating between a feeble-minded person and one of perfectly normal stock will apparently result in normal children although they will be carriers. There is some evidence, however, that such carriers may occasionally show "taints" of abnormality in the form of migraine (nervous sick headache), alcoholism, queerness, violent temper, etc. Thus according to the studies of Doctor Weeks, "In 50 matings where at least one parent is migrainous, there were 350 conceptions, of which number enough is known of 212 to classify 55, or 26 per cent., as epileptic; 12, or 6 per cent., as feeble-minded, with the others tainted or normal. In the 131 matings

where at least one parent is alcoholic, there were 845 conceptions. Of the 494 classified, 151, or 31 per cent., were epileptic; 54 or 11 per cent., feeble-minded, with the balance tainted or normal." Marriage between two carriers will cause the defect to reappear in active form in approximately 25 per cent. of the offspring and 50 per cent. will continue to be carriers.

In a study of 609 case histories of epilepsy by Olive Cushing Smith 336 showed a neuropathic family history, the family histories of 255 were negative (including organic nervous conditions), while those of 18 were unknown. In epilepsy the factor that is most universally present is an inheritable constitutional "peculiarity" of some kind. Such factors as diet, alcohol, injuries or focal infections are probably causative only in a secondary sense in that they operate on a nervous mechanism that is already inherently unstable.

Many Apparently Normal People Really Carriers of Neuropathic Defects.—There is considerable evidence that many apparently normal individuals of our average population are in reality carriers of some form of neuropathic or psychopathic defect, some authorities placing the proportion provisionally at higher than thirty per cent. This being true, then it is easy to explain the apparently unaccountable appearance of epilepsy, feeble-mindedness, or similar defects among the children of what pass for normal stocks. The probabilities are that in many cases it means simply that the parents of the defective children have been carriers. Bad, then, as are the visible, measurable conditions, the disconcerting fact confronts us that as regards feeble-mindedness, at least, they represent only part, possibly the least dangerous part of the situation. When feeble-minded mates with feeble-minded the offspring are all usually feeble-minded. When feeble-mindedness is crossed into normal stocks, the defect in so far as it follows the Mendelian law, may become largely or wholly obscured in the immediately resulting offspring. Nevertheless, it is likely to reappear in later generations, with qualities undimmed. If an individual who carries feeble-mindedness as a recessive marries one who is likewise a carrier, a common occurrence, one out of four of their children will probably be mentally defective, and two out of four may, like themselves, transmit the condition. This explains, for instance, how feeble-mindedness may often appear among the children of apparently normal parents. The most disquieting part of the situation lies in the

fact that in a fairly stable population where a relatively small proportion reveals a recessive defect such as feeble-mindedness, there is always, through contaminations which have gone on generation after generation, a much larger percentage of the population who, though apparently normal, are carriers and therefore transmitters of the defect. Thus such evils are not being confined to the originally defective strains, but are continually thrusting theftuous roots into the better blood.

Without entering into the details of their calculations, it may be stated that two of our most careful investigators in the field of heredity, Professors East and Punnett, have each come to the startling conclusion that, regarding feeble-mindedness as a simple recessive, with 300,000 visible feeble-minded individuals in the United States, with its population of over 100,000,000, there must be between 7,000,000 and 10,000,000 people who are carriers of feeble-mindedness, any two of whom chancing to marry would probably have one child out of four mentally impaired, and two children out of four capable of transmitting mental impairment. This means that even if, in the United States, we could blot out all actively feeble-minded at one stroke to-day, we should still have this enormous reserve of carriers who, marrying as usual, would produce a resurgence of approximately 100,000 active cases in the next generation. It should be noted that these calculations are for feeble-mindedness alone and include neither epilepsy nor the insanities.

The foregoing calculation is based on the supposition that feeble-mindedness is completely recessive in the heterozygote and that therefore when mental defectives appear among the offspring of one feeble-minded and one normal parent the latter was really a carrier. If, however, normal mentality is not always completely or regularly dominant—and, judging from the known fact of incomplete dominance in many cases of Mendelian inheritance, this is not improbable—then the number of families carrying feeble-mindedness as a concealed recessive is not so large as the estimates of East or Punnett would imply.

As matters now stand, however, we not only have the unavoidable increment launched on us every generation through the reappearance of the recessives extracted from carriers but we are doing little to stay the torrent which is issuing from the matings of the plainly feeble-minded, who family for family are apparently out-breeding normal strains. In a recent survey of

certain counties of Pennsylvania Dr. Key discovered that not only was the birth-rate of defective mothers more than twice that of normal mothers, but that the survival ratio of the young of such defective mothers was also more than twice that of the children of normal mothers. Dr. Key found that 60 per cent. of the good-for-nothings, drunkards, criminals, and sex-offenders of the regions studied belonged to ten feeble-minded family strains.

It is becoming more apparent every day as methods of precision are beginning to take precedence over guesswork that many of the "down-and-outers" are not so because of lack of opportunity, but because of inherent incapacity. In the industries this is unquestionably an important factor in the problem of "labor turn-over." For example, in a copy of the *Journal of Delinquency* (March, 1917) before me I find that in a representative group of 107 unemployed men who applied for charity in Portland, Oregon, about one-fifth proved to be of the moron grade of feeble-mindedness, and all were considerably inferior mentally to an ordinary group of successful men. Other studies of similar nature are bringing the same significant facts to light elsewhere in the country. And let us not forget that in a democracy the vote of each of these has just as much weight as that of the most enlightened citizen.

As to the contention that in preventing the propagation of the feeble-minded we may be depriving the world of geniuses, Doctor Goddard remarks: "It is a significant fact that in our three hundred family histories totaling 11,389 individuals not a single genius has been found. Not only are there no geniuses but the fact can not be too strongly emphasized that even the people who are considered normal . . . are not as a rule people of average intelligence. . . ." However, between insanity and genius he finds more kindred spirit.

Cost of Caring for Our Mentally Disordered.—Doctor Charles L. Dana, member of the National Committee for Mental Hygiene, estimated in 1904 that the actual cost of caring for feeble-minded and insane in the United States amounted at that time to \$60,000,000 annually to which should be added the corresponding loss in industrial activity on the part of the afflicted—at least \$20,000,000 more—and he figured that the amount was increasing at the rate of four per cent. per annum. To-day we find estimates of \$300,000,000 as the annual economic loss from

mental disease. This sum does not include provision for mental defect, epilepsy, dependency and delinquency. More than one-sixth the total expenditures of some states is for care of the insane alone. Adding to this economic burden the cost of our mentally disordered delinquents and criminals the total expense becomes stupendous. And further there is the even greater burden of suffering of the unfortunates themselves and the sorrows of those to whom they are dear.

Educational and Psychological Tests and Measurements.—

During the past twenty years keen interest has developed in this country in the matter of so-called "intelligence tests." A number of such tests are now in existence and more are in process of construction. Based for the most part on the Binet-Simon test devised originally for French school children, they are constantly being amplified and fitted more carefully to our own needs. None of them claims to be perfect and most of them although purporting to test native intelligence are not entirely free from the use of information or reactions based on learning or training, but they are probably in the main fairly reliable when properly given and controlled and used in conjunction with other evidence. Most of them with which the author is familiar seem scarcely to do justice to the slow reflective type of mind as against the more versatile type. It is rather unfortunate that the scales of most of these tests, for adults as well as for the young, are expressed in terms of the mental age of children, for such comparisons may be very misleading. However, the tests were first tried out and standardized in schools and no better yard-stick seems to have presented itself than the age-levels of children.

Professor Woodworth in defense of intelligence tests gives the following reasons for believing that such tests do distinguish between people of lower and higher intelligence.

"1. As a child advances in age from 3 to 14, he also advances in his success with the Binet and other tests.

"2. Children who advance rapidly in school test high, children whose school progress is slow and difficult test low.

"3. Boys who test high can swing college studies, others not.

"4. In the army, officers tested from high to fairly high, while enlisted men scattered all the way from high to low, with the great mass in the medium grades.

"5. In a skilled trade, proved experts test higher, as a rule, than the lower grade men.

"6. Test any two men, one of whom in his achievements, conversation and behavior generally, evinces much higher intelligence than the other, and you will find the test results to correspond fairly well with this fact. This is the sort of evidence that must be met by those who desire to thrust aside the intelligence tests."

The attempt in all is to obtain quantitative values for various mental and temperamental qualities and processes. Since there is no such thing as absolute intelligence such scales are obviously relative in nature and what they show is differences in degree—the spread of intelligence—rather than absolute values.

By far the greatest single effort at mental measurement in America—and the only considerable attempt to measure adult intelligence, anywhere—was that made on the recruits in the United States Army during the World War when more than 1,700,000 men were tested. The result showed that the average man of the draft was on a par in mental ability with the average boy of thirteen and a fraction. Men exempted because they were essential in industry were not tested and it is believed that their inclusion would have raised the level slightly, so that it is generally inferred that the army rating indicates that mental majority is reached about the age of fourteen. This does not mean, of course, that a boy of fourteen knows as much as he ever can know. In the words of Professor Woodworth again:

Intelligence tests "are not designed to measure special knowledge or skill acquired in education or the trades, nor the knowledge of the world that can only come from long experience. They aim to measure the individual's capacity to learn by experience, to adapt himself to new situations, to see the point of new problems and to reason them out. Mental alertness and suppleness, keenness, accuracy, quickness and control are what they seek to test. Intelligence in this sense might remain constant from the age of 14 on and still the individual might continually advance in knowledge and skill. Intelligence might even slowly decline and still the individual be advancing in mastery of his own chosen lines of endeavor."

Prepared by a committee of the American Psychological Association and of the National Research Council, the army tests were thoroughly tried out in four National Army cantonments and successively revised and improved to increase their practical usefulness. Then under the direction of Robert M. Yerkes, they

were applied in the army at large with the exception of some of the industrial or vocational divisions. Three forms of individual tests were used: The Yerkes-Bridges Point Scale, the Stanford-Binet Scale, and the Performance Scale. The tests were intended to discover what each individual conscript was best fitted to do as his part toward winning the war. While these tests can be and have been criticized from many points of view, the fact remains, when all is said and done, that they are statistically valid. The best evidence of their reliability is the closeness with which the later performance of many of the tested individuals corresponded with the forecast. They were not tests of schooling or of memory, but were intended to be tests of intelligence, power to reason, to see relations, to grasp situations as a whole. These are largely inborn qualities. There were two sets of tests: one, the *alpha*, for men who could read and write English readily, the other, the *beta*, for the illiterate, the non-English speaking, and those who could not read and write English well. The results were tabulated according to a scale which ranged from A to E, in which A and B were regarded as superior, C as average, D as inferior, and E as very inferior. Of our white recruits, only 12 per cent. proved to be superior, 66 per cent. were average, and 22 per cent. inferior. As with other such tests these were expressed in terms of mental age based on comparisons with school children. While such comparisons do not tell the full story of the respective abilities of adults and school children, graded at the same level, to be self-supporting and even socially valuable citizens, nevertheless such a scale is of value in classifying individuals according to their relative mental capacities. It at least shows the spread of the capacities tested. It is a momentous fact that 47.3 per cent. of our white recruits graded below the mental age of thirteen years. And unquestionably the army possessed a higher average of intelligence than would be found among the same number of individuals taken at random from our population, because the obviously feeble-minded and those who were otherwise mentally defective had already been weeded out before the tests were made. Yet, the fate of a democracy must be determined by the intelligence of its voters, and we may well remember also that intelligence can not be bestowed by a majority vote.

How extensive the literature is on mental testing is shown from a bibliography recently issued by the Bureau of Education of

the United States Government (Bulletin No. 55) comprising 233 pages with about 25 titles to the page.

The Backward Child in School.—It is only in recent times that we have come to realize the seriousness of the problem which the backward child presents in our schools. It is of the utmost importance to discover early in school life which of the backward children owe their condition to adenoids, defective sight or hearing, poor nutrition, imperfect circulation, or other remediable defects, and which are the victims of innate mental deficiency. The treatment of the individual must be very different in the two cases. In the one the condition can be cured by proper manipulations or other treatments; in the other it can only be ameliorated. All school children who are two or three years below grade should be rigidly inspected by the medical examiner.

From a study of about two thousand children comprising the first five grades of an entire public school system Goddard found that eighteen per cent. were definitely "backward." Of these between two and three per cent. were actually feeble-minded, the condition in the remaining fifteen per cent. being presumably capable of correction. Other similar surveys have given practically the same results. A committee of the American Eugenics Society has estimated recently that there are some five million children in the United States who could not go through the lower grades of school and about twenty million who have not sufficient intellect to get through grammar school.

The Exceptionally Able Child Likely to Be Neglected.—However, while we must not forget that it is important to recognize backward children and to see that they are segregated into small groups which are not required to do the full amount of work in regular time, it is equally urgent to see that the unusually bright individual is also given opportunity to advance more rapidly than the rank and file. Only too often the holding back of a child in school leads to lack of interest and habits of mental laziness, and sometimes to truancy and incorrigibility. The general attempt in our graded schools to keep all children close to the average is to be strongly condemned.

Professor Yerkes believes that in the present state of our psychological and educational knowledge a child can be placed with assurance and to advantage into some one of five classes and given attention according to his particular needs or qualifications. These classes are: (1) The intellectually superior or

supernormal; (2) the mentally normal, typical or average; (3) the intellectually dependent; (4) the intellectually inferior or subnormal; (5) the affectively or instinctively defective. While recognizing that available statistics are insufficient to justify dogmatic statements, he believes the indications are that in every hundred of the school population 4 to 6 children will be found intellectually superior, 4 to 6 intellectually inferior, 1 or 2 intellectually dependent and 1 or 2 affective deviates. The remaining 84 to 90 individuals constitute the mentally normal, typical or average.

Importance of Rigid Segregation of Feeble-Minded.—As regards the really feeble-minded little can be done beyond making them as happy as possible and developing the limited gifts they have been given by nature. Their teaching must be in the main concrete and simple. At the age of puberty it is imperative to see that the sexes are separated and kept under sufficient permanent supervision to prevent all possibility of procreation. There is neither economic nor common sense in even allowing the remotest chance of such occurrences as the following: "This is the case of a feeble-minded and epileptic woman who had six children by various persons while an inmate of a county poor house. One child at the age of eighteen died in the almshouse, two died in infancy, one was epileptic (the son of a man with a criminal record) and two who are now living in the almshouse are feeble-minded, one being the son of a negro." Again, we find a superintendent of an English almshouse reporting that one hundred and two out of one hundred and five children born there in five years were feeble-minded.

As conditions are to-day every institution for the feeble-minded has a long waiting list and the same is true of most asylums for the insane. Instead of providing the prolonged care necessary for such patients, institutions are forced to discharge many prematurely in order to make room for more urgent cases.

In Ohio, for example, we find from a booklet published by the Cleveland Chamber of Commerce that of the 34,500 feeble-minded in that state at least 15,000 are in need of institutional training, although their one institution for the feeble-minded cares for only about 3,000. This condition can be duplicated in practically every state in the Union.

The problem has got so far out of hand that it is now seemingly impractical to attempt the permanent segregation of all

feeble-minded into institutions or colonies. The best that can probably be hoped for is that they can be given special training in appropriate institutions and then be returned to the community, provided with the kind of work they can do, and kept under proper supervision. If parenthood is to be prevented and further serious contamination of our race avoided, certain of these mentally eclipsed unfortunates must be segregated through the reproductive period into colonies for the separate sexes. To be sure the undertaking is stupendous, but the problem is not one which will stand still while we deliberate about ways and means of doing something at some indefinite future day. It is a menace to our very life blood as a nation.

Colossal as the undertaking seems, as a matter of fact, the initial cost would be the greatest item of direct outlay, for such colonies, once established, can by wise management be made largely or wholly self-supporting. We have considerable evidence based upon the actual experience of well-managed institutions that most feeble-minded persons under proper supervision can do much work that is helpful to the institution or the state and healthful for themselves. Data from various sources all agree in showing that the economic value of the feeble-minded, above the grade of imbecile, is more than the cost of their care and maintenance. A recent example is that of twenty-five boys from one of the New York State custodial asylums, who were sent up into the Adirondacks for a month of camping, and given a lot of seedless spruce to set out. They did their work in a spirit of play, and yet at the end of their visit they had reforested a considerable area. A fair estimate placed the net value of the work to the state at \$1,000, yet the cost of their transportation and keep for the entire period amounted to only \$400. The fact is that many feeble-minded individuals are physically strong, good-natured, irresponsible children, who remain happy and contented if kept under reasonably comfortable conditions. It should be borne in mind, moreover, that with the reduction of the feeble-minded there would also be a lessening in our expenditures on paupers, criminals, inebriates and delinquents.

Importance of Early Diagnosis of Insanity.—In insanities, even when of hereditary origin, there is much hope in certain cases of greatly benefiting the individual, though a permanent cure, or at least the establishment of procreative fitness may be impossible. It is extremely important that the public realize how

much can be done through early examination and advice in such mental afflictions. Most of the insane who recover usually do so within a few months of their first alienation, hence the importance of losing no time in detecting the condition and securing early treatment. It is now well known that many cases of chronic insanity may be measurably improved under the care of a psychiatrist by systematic re-education, especially in industrial lines. But how little of this may be expected at the hands of the untrained custodians who "feed" the inmates of our county almshouses, to which in many states the chronic insane are entrusted, is obvious.

All Insane Should Be Passed upon by Competent Psychiatrists.—The atrocious system of turning the chronic insane over to county poorhouses manned by supervisors whose chief qualification for the position has not infrequently been the lowness of their bid for boarding and caring for the inmates, can not be too strongly condemned. Incredible as it may seem, in some states the court can on its own judgment send patients directly to these institutions without first submitting them to the study of expert physicians in the state hospital for the insane. The viciousness of such procedure is evident when one realizes that often careful scrutiny on the part of the very best experts, extending over a considerable period of time, is required before the true condition of the patient can be determined. Recently a psychiatrist of high standing, who was gathering data on county asylums for a national organization, informed the writer that beyond the shadow of a doubt he had come across case after case in county asylums which would have been curable under proper treatment.

Here again the responsibility in last analysis must rest upon us as citizens, for it is largely through our intelligent demands as voters that conditions will be improved and competent experts be put in charge of county asylums as well as of the state hospitals for the acutely insane.

Importance of Heredity in Insanity Not Appreciated.—We have already seen that heredity plays an important part in insanities. There can be little doubt that the tendency is to underestimate rather than over-estimate its importance. Many cases said to be "caused" by mental strain such as those occasioned by domestic infelicities, business reverses and the like should in all probability be fundamentally attributed to something far

more deep-seated than the more obvious cause. In many such instances there is little doubt that an inherent weakness in mental make-up exists which predisposes the individual toward mental breakdown. This is more apparent when one recalls that there are thousands of other individuals who undergo equally great or greater calamities without loss of mental balance. There are well-recognized types of mental disposition which later contribute to corresponding forms of insanity. In many instances the final catastrophe may be averted if the "peculiar" individual can be kept in good health and guided into right habits of thought. Undoubtedly certain infectious diseases, arterio-sclerosis, various poisons in the blood, childbirth, and similar influences often enter as important contributory factors. In all cases of cure, however, we must face the fact that under existing conditions these mentally restored individuals are released into society without let or hindrance as regards their marital relations.

CHAPTER XX

CRIME AND DELINQUENCY

The Relative Importance of Heredity and Environment in This Field Uncertain.—The whole question of crime and delinquency is a highly complex one. Here, perhaps, more than in any other phase of race betterment we find the greatest difficulty in separating the effects of hereditary predisposition from the results of unfavorable environment. While there is no longer a reasonable doubt about such nervous disorders as epilepsy, feeble-mindedness and certain forms of insanity being rooted to a considerable extent in ancestral taints, the degree to which crime or delinquency is based on heredity is far more questionable. Every student of genetics knows that we may have dwarf plants because the constitution of the germ is of a nature to produce only such individuals, or we may have dwarfed plants because of adverse conditions of soil and lack of an opportunity to climb or rise to their full capacity. Bateson pertinently remarks, "The stick will not make the dwarf pea climb, though without it the tall can never rise. Education, sanitation, and the rest are but the giving or withholding of opportunity." The important sociological question for us to determine is which of these lowly peas of the human family are really dwarfs and which are dwarfed simply because the stick of opportunity on which to climb is lacking.

Beyond doubt a considerable portion of crime and degeneracy is due in some measure to innate inclination, but with just as little doubt much is the effect mainly of vicious habits acquired through an unwholesome environment. A normal appetite or impulse may be given a pathological trend by bad influences. And one has to reckon, moreover, with degrees of hereditary aptitude to crime. Just what is the measure of normality? To what extent by developing to their highest point certain inhibitive or opposing tendencies, can we counteract certain inherent proclivities for wrong-doing? By what means shall we sift the congenital defectives from the victims of suppressed opportunities? These and kindred questions confront us at the very outset of

our studies of crime and delinquency. It is obvious that although we may institute the strictest elimination of the socially unfit, unless we can provide a wholesome environment for the fit, lapses into unfitness are sure to recur.

Percentage of Crime in the United States.—As regards crime, when we compare the United States with other nations, the result is appalling. We have a crime record which is far in excess of that of any other civilized country and which is seemingly unparalleled in the history of the civilized world. Murder is twice as prevalent in the United States as in Italy, the next worst offender; thirty-six times more prevalent than in Switzerland; and eighteen times more prevalent than in Scotland. In 1922 with an estimated population of about 58,000,000 Japan had 461 homicides, but in the United States with twice the number of inhabitants there were more than 10,000 homicides, or ten times as many per unit of population. In the year 1916 London, with a population of more than 7,250,000, had only nine premeditated murders, while Chicago, with about one-third the population of London, had 105 such murders; that is, nearly twelve times as many. In all England and Wales, with 40,000,000 people in 1923 there were less than 200 killings, but we find St. Louis alone surpassing this record in 1924. In 1918 Chicago had twenty-two robberies for every one in London. In a paper before me bearing the date of October 7, 1925, one reads regarding the Chicago district: "murder continues in Cook County at the rate of more than one a day. In the last 279 days there were 288 murders." While doubtless a number of these should be classified as manslaughter rather than murder, a reckless disregard for human life is none the less evident. From 1916 to 1918 Glasgow had 38 homicides, while Philadelphia, but slightly larger, had 281. Cleveland, one-tenth the size of London, had three times as many homicides in 1917. And so, year after year, the score reads for various other American cities.

Frederick L. Hoffman, Consulting Statistician of the Prudential Insurance Company of America who for years has prepared annual homicide records for American cities (deaths from homicides alone certified to as such on the standard death certificates) in 1925 concludes a survey of *The Homicide Problem* in part as follows:

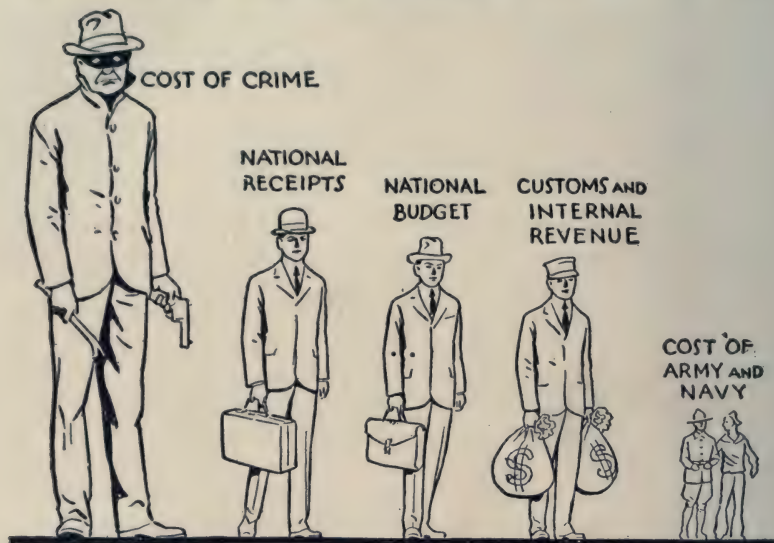
"Deaths from homicide in American cities reached the highest rate on record during 1924. The rate for twenty-eight American cities with about 21,000,000 of population for 1924 was 10.3 per 100,000, which is almost exactly double the rate of 1900, or twenty-five years ago. Anticipations that the rate had reached a maximum point during 1923 were not realized. The murder situation in America, in other words, is worse than ever. An analysis of the figures for the last six months of 1924 compared with the first six months indicates that the trend is still distinctly toward greater frequency. There is hardly a day on which the country is not shocked by some conspicuous murder case, which, however, is of less importance than the large number of murders which do not attract wide-spread attention. There is no question of doubt but that the annual toll of murder now exceeds 11,000. But the recorded toll unquestionably falls short of the actual facts in view of the increasing extent to which the evidences of murder are cleverly disguised. . . ."

The Cost of Crime.—How many of us realize that in the United States crime costs us annually at least twelve times as much as our combined army and navy and over three times the amount of our total internal revenue and customs receipts? In a recent article in *Business*, published in Detroit, Edward H. Smith shows that the cost of crime in our country is at least ten billion dollars annually (Fig. 94, p. 368). This is more than two and one-half times the total national receipts for 1923 and three times the national budget for the same year. His figures have been gathered over a number of years from such sources as the police departments of our larger cities; the New York Stock Exchange; the Association of Railway Executives; the National Surety Company; the Insurance Company of North America; the National Vigilance Committee of the Associated Advertising Clubs of the World; the National Association of Credit Men, and kindred organization.

Feeble-mindedness Often a Factor.—The conviction is steadily growing among students of human heredity that a considerable amount of crime, gross immorality and degeneracy is due at bottom to feeble-mindedness and that, therefore, if we can once eliminate feeble-mindedness, these vicious accompaniments will at the same time in equal measure disappear. Goddard, for example, one of our authorities on the inheritance of feeble-mindedness, is convinced that a large proportion of the delinquent girls who fill our reformatories are actually feeble-

minded. They are often the higher grade or moron type, and their mental condition remains unsuspected because they have never been thoroughly tested in this respect.

Probably, however, not more than 10 per cent. of the feeble-minded have particularly vicious potentialities, and this ten per cent. is made up largely of the type already mentioned (p. 334) which should really be classified as "affective deviates" rather than feeble-minded. The chief difficulty with the feeble-minded proper, from the standpoint of crime or delinquency, is their



THE CRIME COST TWELVE TIMES THE PRICE OF PEACE

FIG. 94

As the diagram shows, the country's crime cost, about \$10,000,000,000 annually, is two and a half times the total ordinary receipts for 1923, three times the national budget for the same year, more than three times the customs and internal revenue receipts, and at least twelve times the annual cost of the Army and Navy (from *The Literary Digest*).

lack of self-control. They yield easily to suggestion or temptation and thus constitute recruits for delinquency rather than a type which has a downright urge toward crime.

Many Delinquent Girls Mentally Deficient.—According to Havelock Ellis, 2,500 of some 15,000 women who passed through Magdalen homes in England were definitely feeble-minded and

were known to have added a thousand illegitimate children to the population.

The reports of the so-called white slave investigations in New York City classed 25 per cent. of these unfortunate women as mentally incapable of taking care of themselves. Other investigations indicate that from 40 to 60 per cent. of this class of women are defectives. For example, from the report of the Massachusetts "Commission for the Investigation of the White Slave Traffic, So-Called," one reads: "Of 300 prostitutes, 154, or 51 per cent., were feeble-minded. All doubtful cases were recorded as normal. The mental defect of these 154 women was so pronounced and evident as to warrant the legal commitment of each one as a feeble-minded person or as a defective delinquent. . . . The 135 women designated as normal, as a class were of distinctly inferior intelligence. More time for study of these women, more complete histories of their life in the community, and opportunity for more elaborate psychological tests might verify the belief of the examiners that many of them were also feeble-minded or insane."

The data from some of our public reformatories, industrial schools and state homes for delinquent girls, are very instructive in this respect. Reports from a number of such institutions show that many of their inmates are mentally subnormal. The proportions range from 33 per cent. in the New Jersey Reformatory at Rahway to 89 per cent. in the institution at Geneva, Illinois.

Institutional Figures Misleading.—However, significant as are these figures from institutions for delinquents, one should not be misled by them. They are undoubtedly not representative of offenders in general, but of a selected group of the most hopeless cases. In the first place the more capable individuals escape the dragnet which lands the defective delinquents in an institution, and furthermore, because of liberal systems of probation, only the more incorrigible or the very stupid make up the bulk of the population of such places. Miss Augusta F. Bronner, assistant director of the Psychopathic Institute of the Juvenile Court of Chicago, from a careful study of five hundred and five cases of delinquent boys and girls in the Detention Home, chosen with as little selection as possible, found the proportion of mentally subnormal among them to be less than 10 per cent.

Many Prisoners Mentally Subnormal.—Doctor Walter S. Fernald, formerly of the Massachusetts School for Feeble-

minded, estimated that "at least 25 per cent. of the inmates of our penal institutions are mentally defective." Among the various available estimates at hand this seems to be a fairly conservative approximation. Hastings H. Hart points out that this calculation of 25 per cent. means that there are 20,000 adult defective delinquents in prison, and 6,000 youths in juvenile reformatories, or a total of 26,000 in custody of the United States.

Dr. William J. Hickson, Director of the Psychopathic Laboratory of the Municipal Court of Chicago, as the result of examinations of over 42,000 cases of criminals and suspects is convinced that mental unsoundness or mental disease of some type is by far the most responsible factor in crime and that such mental disorders are mainly of the inheritable forms. Concerning the latter point he remarks as follows:

"An example of the stressing of environment as against heredity was recently seen where an investigator attributed most of the immorality, morbidity, delinquency and dependency of children to the low wages of the father, adding that higher wages was the solution of the problem, thus entirely overlooking the influence of heredity and its relations to mental and physical defectiveness and not at all concerned with the question as to why the earnings of the fathers and mothers of these unfortunates are so low, why they are idle so much of the time, why they are alcoholics, deserting, neglecting and abusing their families and why there is not the proper educational and parental supervision, etc.; not in our opinion that such supervision makes much material difference for if the parents are defective so also the children, and our daily experience teaches us how numerous are those rising above their environment as well as those sinking below it."

And he concludes that "The entire history of criminality as far back as we can go points unmistakably to but one conclusion, and that is that from time immemorial defectiveness and crime have been synonymous." He feels convinced "that the factor responsible for a large percentage of social service work lies in that two per cent. mentally defective group of our population representing feeble-mindedness, psychopathy or both, which group keeps the other ninety-eight per cent. busy looking after it. . . . It is this ever-present two per cent. that confronts the social worker at every turn, whether in dealing with crime, dependency, alcoholism, unemployability . . . etc."

While there is no way at present of arriving at a wholly correct estimate regarding the respective parts of heredity and environment in the production of crime, it is evident at least that mental disease or mental deficiency is a highly important factor and it goes without saying, therefore, that every capital offender or recidivist should be given a thorough psychiatric examination. It is also obvious that such medico-legal examination should be made by an impartial committee of alienists attached to the court rather than by sets of "specialists" hired to make a case for or against the offender.

In a study of 10,000 prisoners in various penal and correctional institutions in various states, at least 60 per cent. were found to be classifiable in terms of some form of abnormal mental health. In Texas, for instance, only 29.4 per cent. of the 3,451 prisoners in the state penitentiary and only 14.2 per cent. of the 226 inmates of 18 county jails could be classified as mentally normal. Again, in a study of 1,288 inmates of 34 county jails and penitentiaries in the state of New York, 76.6 per cent. showed some form of mental deviation.

From the reports of surveys made in eleven states during recent years by the National Committee for Mental Hygiene one learns further that more than half of the population of penitentiaries and three-fifths that of county jails showed definite mental anomalies. The classification of the abnormal conditions was as follows:

	<i>Penitentiaries</i> (8,581 prisoners examined) Per cent.	<i>County Jails</i> (3,206 inmates examined) Per cent.
Mentally diseased or deteriorated.....	4.9	4.9
Epileptic	0.7	1.3
Psychoeurotic	1.2	1.2
Psychopathic	18.6	27.4
Mentally defective	12.5	13.9
Border-line defective or subnormal.....	14.4	11.7

The Recidivist.—In houses of correction, penitentiaries and jails the problem of the "repeater," technically termed the *recidivist*, is a serious one. Massachusetts found in 1924 that 48.6 per cent. of the inmates of its house of correction had served previous sentences and that 19.5 per cent. of these had been sentenced from 6 to 15 times. A recent survey of 1,288 prisoners in 34 county jails and penitentiaries of New York State showed 23 per cent. to have at least average intelligence and to be free

from nervous or mental disease; 77 per cent. psychopathological individuals of well-recognized types; and 66 per cent. of the total number were recidivists. Of those who had been arrested only once, 64 per cent. were mentally abnormal but of those arrested four or more times 90 per cent. were mentally abnormal.

What Is Meant by a Born Criminal?—On attempting to answer this question all we can do is to fall back on the assurance that any act directly or indirectly injurious to society is an offense, and that those offenders who are congenitally unable to distinguish between what is generally accepted as right and wrong, or who if recognizing this are nevertheless uncontrollably impelled toward or are unable to refrain from antisocial acts because of some inherent condition of intellectual or volitional make-up, may be legitimately classed as individuals born with an aptitude for crime and social transgressions. In such individuals the natural mental make-up is lacking in some of its necessary elements so that memory, judgment, or will-power are not up to the minimum that is necessary for the establishment of proper conduct. In some cases, apparently, this lack finds expression in almost any kind of vice or crime into which circumstances happen to lead the individual. In others, however, there seem to be tendencies toward the commission of certain types of crime or vice. Certain family strains are characterized by petty thieving, others by deeds of violence, and still others by sexual offenses. Certain types of mental defect are closely associated with certain crimes. Thus, sufferers from incipient paresis seem particularly prone to commit assaults and larceny; epileptics, crimes of brutality and violence.

The Epileptic Criminal Especially Dangerous.—One of the characteristics of epilepsy, indeed, emphasized by various psychiatrists, is that frequently it leads to loss of those forms of self-restraint which are absolutely indispensable to morality and the safety of society. Cruelty, atrocious sexual offenses and other vicious crimes are the result. It is a noteworthy fact, moreover, that often in the milder forms of the affliction, where instead of well-marked convulsions only momentary lapses of consciousness occur, the greatest amount of mental and moral deterioration and fluctuation is sometimes found.

The situation as regards the epileptic is well presented by Doctor William Healy, former Director of the Juvenile Psychopathic Institute of Chicago, in an article entitled "Epilepsy and Crime;

the Cost," in the *Illinois Medical Journal*, November, 1912. He says:

"In the work of our institute,* which represents the most thoroughgoing research into the genetics of criminalism ever undertaken in this country, we have with the help of parents and others carefully studied nearly 1,000 young repeated offenders. We have found that no less than $7\frac{1}{2}$ per cent. of these are ordinary epileptics, and we have reason to suspect others. This by no means represents the total number of epileptics seen in connection with juvenile court work, where, of course, first offenders as well as large numbers of dependents are seen. In addition to my above enumeration, other cases seen by the Detention Home physicians and myself mount up to many scores of cases. If one remembers that it is ordinarily calculated that one person in every 500 is epileptic, the significance of this high criminal percentage is clear, and the practical bearing of it is still further accentuated by the fact that some of the worst repeaters are epileptics, and that many of the gravest crimes are committed by these unfortunates. The connection between epilepsy and crime has everywhere been recognized by students of the subject, but it apparently needs constant emphasis in order that common sense steps may be taken toward guardianship of those who suffer from a disease which wreaks such extravagant vengeance on society."

Mental Disorders Most Frequently Associated with Crime.

—Doctor Charles Mercier, an English authority on crime and insanity, in enumerating the mental disorders most frequently associated with crime, places the insanity of drunkenness first. Any one who will take the trouble to verify the facts in his own community will find that a large percentage, frequently considerably over half, of the arrests made by the police are for acts committed while the offender was more or less under the influence of alcohol. Next to drunkenness among mental disorders which lead to crime Doctor Mercier places feeble-mindedness. Next to feeble-mindedness comes epilepsy; then paranoïa or systematized delusion; next paresis; and lastly melancholia.

Paranoïcs are peculiar in that they are particularly apt to attack persons of prominence. Highly egotistical, they almost invariably believe themselves or some one or some cause dear to them, the

* The Psycopathic Laboratory in connection with the Juvenile Court of Chicago.

subject of a plot, perhaps to rob them, to torture them, to steal their invention or literary productions, or to persecute them in some way. Two if not three of our murdered presidents owe their assassinations to paranoics. Many rulers have been attacked and some killed by such insane individuals. Most of the "cranks" who write threatening letters are lunatics of this type.

Of the kinds of mental unsoundness known to be inheritable which are of special significance from the standpoint of crime and delinquency, undoubtedly feeble-mindedness ranks high. We have already seen that as our methods for detecting the higher grades of feeble-mindedness become more accurate we disclose in border-line cases a veritable hotbed of mental incapacity suitable for the engendering of the criminal and the vicious. Here in addition to some of the more pronounced criminal types belong hosts of our chronic petty offenders, our sexually vicious and our "won't-works." One interesting outcome of a recent investigation into the army of unemployed in England was the discovery of the general unfitness of these unemployed. In our own country the habitually unemployed are so not because of lack of work, but largely because it is unprofitable to employ them.

Sexual Vice.—As to sexual vice, the skein is indeed a tangled one. Since nine-tenths of the difficulty centers in a lack of self-restraint, and inasmuch as the mating instinct is one of the strongest that tugs at the flesh of humanity, it is obvious that those by nature deficient in volitional control will almost without exception give way to the call. So as might be expected the hordes of our feeble-minded and epileptic are always a source of grave danger in this respect. However, the mentally enfeebled are by no means the only offenders; indeed, they are probably not the majority. The true situation is finally dawning on society and the reformer's call for instruction in "sex-hygiene" resounds through the land. The whole matter is one of the most perplexing and momentous that confronts us to-day.

The Question of School Instruction in Sex-Hygiene.—While the writer does not for an instant underestimate the gravity of the situation, and has only contempt for the nonsense that is palmed off on children about their origin, or the indelicate self-consciousness which puts under the ban the discussion of so serious a problem by adults, still he is not convinced that the universal teaching of the subject to children in schools by the

average teacher, as advocated by some, is to be the solution of the matter or is even a wise attempt at solution. Yet he freely admits that he is possibly overfearful of the effects of the undesirable features of such instruction. True it is that all children do learn, frequently at an astonishingly early age, about sex, and their knowledge is usually of an undesirable kind from unreliable and often vicious sources, and it is equally true that parents, either through ignorance or prudery, generally can not be depended on to give the child necessary instruction. But before entering on a wide-spread campaign of undiluted sex-instruction in schools might it not be more prudent to make an attempt toward reaching fathers and mothers and convincing them of the necessity of dealing more frankly and intelligently with their children regarding sex?

Even to the novice in psychology the powerful nature of suggestion is known, and with this knowledge before us, is it not wiser to strive in the main to keep the child's mind off of sex rather than specifically to focus it on it by special convocations and discourse. If our psychology means anything, then the worst possible thing we can do for a child is to make him unduly sex-conscious. Something might be done profitably perhaps in schools in an unobtrusive way by specially gifted persons, but the self-conscious way in which most teachers go about topics of sex is certainly not reassuring to the thoughtful observer as regards the benefit derived from such instruction. The one evident method of accomplishing wholesome sex-instruction in schools, devoid of all possibility of undesirable suggestion and sex-consciousness, is in the form of biological work where plants and animals are studied in all their relations, the subject of propagation being taken up in as matter-of-fact a way as the functioning of any other organ system of plants or animals. In such a course, long before the subject of sex in higher animals need be approached the pupil will have developed an attitude of mind which will lead him to see nothing unusual or suggestive in the function of sex no matter where it may be found. Incidentally, inasmuch as the manner in which germs affect living organisms should be studied in such a course anyway, it would be a simple matter to give all necessary information about the dangers of infection from venereal diseases.

Mere Knowledge Not the Crux of the Sex Problem.—However, desirable as correct knowledge about sex is, knowledge

alone is not the crux of the sex problem. The moral dangers and abuses that we are trying to circumvent lie rather in the realm of the emotions than that of the intellect. The problem must be solved from a broader foundation than mere information. The all-important consideration is the early establishment of general habits of self-control so that these may become incorporated in the nervous organization of the child and become inhibitory anchors against passions and temptation. Children must be taught to suppress the present impulse, to sacrifice the immediate pleasure for the more distant or permanent good. They must be practised in calling up feelings that will counteract other promptings which if followed blindly are inimical to social welfare. Their control must come from within, not as a matter of external compulsion. That way character lies.

So in viewing the problem of sexual hygiene the writer feels that our attempts toward damming the torrents in the adolescent by a belated effort at verbal instruction in sex-hygiene is at best only a palliative or an attempt to cure the symptoms of a more deeply-seated, organic, social malady. The treatment should have been in progress long before in the form of training in self-control, and in the inculcation of the sense of dignity and self-respect which springs from the individual's consciousness of being, not a slave to his desires, but his own master. This, together with the judicious schooling of boys in a greater chivalry and respect for womanhood, and of girls in the necessity of meriting such esteem, will, in my estimation, carry us further than formal courses in sex-hygiene.

Early Training in Self-Restraint an Important Preventative of Crime and Delinquency.—As to crime and delinquency in general, it is evident that the same early training in self-restraint is a most important factor of prevention. A wise warden in charge of a large prison says, "Most of these men are here because they have not learned sufficiently the lesson of self-control." This is the age of preventive medicine, why not also of preventive crime and delinquency? Instead of confining our practise to punishing offenders, necessary as this may be under the present conditions, why not strive more to prevent the commission of offenses? As far as normal individuals are concerned much can be done by early cultivation in self-discipline and through the establishment of moral back-bone by training in

the overcoming of difficulties. Much, very much, also remains to be done in the correction of wrong social conditions.

Unpardonable to Permit Delinquent Defectives to Multiply Their Kind.—As for our mental defectives and moral imbeciles, knowing now how strongly hereditary the underlying factors of these conditions are, and with no preventive or curative agents in sight, to let them produce progeny is clearly unpardonable.

CHAPTER XXI

POPULATION

Reproductive Pressure.—It is a well-established biological principle that every species of plant and animal lives under a reproductive pressure which tends to overpopulation. Like gas in a vessel any living species expands into adjacent territory the minute a rift appears in the restraining wall. Remove a single environmental check, animate or inanimate, and in a short time, often in a single generation, the species fills the new bounds. Man is no exception in the animal kingdom. He tends in time to occupy any given area to its limit of support for the type of culture then prevailing. Any shift from a more primitive to a more advanced culture—hunting to pastoral, pastoral to agricultural, agricultural to industrial—is always followed by an increase in population. Because of his food reserves and his better conditions of life civilized man, along with his cultivated plants and domesticated animals, is probably more fecund than were his primitive ancestors.

In the past few years a number of stimulating books on the problem of population have appeared and a wide-spread popular interest in the subject has been aroused. Intelligent people are recognizing as never before the prominent part played by overpopulation as a cause of war. Plainly, undue crowding means pressure for expansion. New territories are needed for the excess of people and as additional sources of food, or what amounts to the same thing, new markets are required in which surplus manufactured products may be exchanged for food. For eloquent testimony to this fact one has only to witness the emphatic utterances of Mussolini, the uneasiness of Japan and the general mad scramble of European nations for mineral and other natural resources. So long as unpopulated or sparsely populated lands are available for overflow, while there may be considerable local jostling and discomfort from time to time, the world as a whole moves complacently along in its hit-or-miss fashion without undue tension. The fact remains, however, that the earth's surface and the earth's resources are strictly limited, that sooner or later

there can be no more expanding and the final day of reckoning must come. Considerable compacting can thus be accomplished through occupational balancing but such adjustment is merely palliative. While an industrial society permits of a much greater density of population in special areas than an agricultural one, obviously agricultural productivity is the final arbiter of world population.

Since the famous essay of Malthus a century and a quarter ago which maintained that, except as checked by famine, disease or war, population tends to expand in multiplicative ratio while the means of living—food, clothing and the like based on agriculture—increases only in an additive way, the problem of population has been more or less to the fore. The inevitable outcome, according to Malthus, unless population is deliberately restricted, is war, crime, poverty, vice and general human misery.

The sequel has shown that Malthus fell short of quantitative accuracy in his contention that means of subsistence can increase only in simple additive ratio, for it has long since become evident that improvement in methods or in skill results in increased yield for the same amount of labor, and that availability of food and other necessities of life through ready distribution plays an important part in determining how many individuals can be supported in a given area. There are obvious limits, however, to the ameliorations possible through such aids and the net result is merely a postponement of the inevitable. To-day we hear less about arithmetical ratios and more about the *law of diminishing returns* in both agriculture and industry, but however we label the limiting factor, the important thing to realize is that there is a limit.

The Curve of Population Growth.—Professor Raymond Pearl has found as the result of a careful statistical study of the available census enumerations of some twenty different countries that the same type of equation mathematically describes the growth in all cases. Irrespective of cultural conditions, racial composition or industrial development, the trend of their respective populations—after minor irregularities due to temporary fluctuations in birth-rates, migrations and the like are smoothed out—tends to follow the same curve of development. He shows, furthermore, that this curve of population growth is the same as that for the growth of an individual, or of a city, or a population of yeast cells, or a colony of fruit flies in a culture jar.

He has thus approximated in a striking manner a biological law of population growth.

The curve (Fig. 95, below) is roughly a stretched-out S. Rising slowly from the horizontal, with increasing rapidity it approaches the vertical, then reverses and trails off toward the horizontal. Interpreted biologically this means that at first an abundance of upbuilding or constructive factors prevail which lead to an ever accelerating growth, but that ultimately restrictive bounds are encountered which come more and more into prominence until equilibrium is reached. Presumably the most

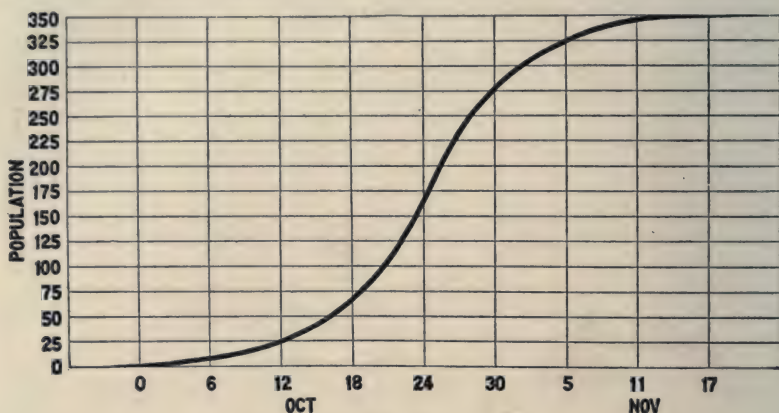


FIG. 95

Increase in a population of fruit flies in a pint milk bottle. (From Shull, modified from Pearl.)

favorable relation between inhabitants and sustenance is that in which the rate of growth reaches its maximum.

Some of Professor Pearl's curves are reproduced in (Figs. 95 to 98, pp. 380-383). The small circles in the diagrams indicate known census counts of population; the heavy solid line shows for each country the fractional curve afforded by these counts and where it fits into the standard curve; the dotted portions of the curve indicate its extension as deduced from the known part.

The curve for the fruit fly (*Drosophila*), an organism used extensively in genetical studies because of its remarkable suitability for laboratory experimentation, is shown in Fig. 95, above. This fly has a short life cycle and breeds abundantly. The female

lays from a few to as many as 25 or even 50 eggs a day for a period of at least 10 days. The eggs hatch in from 24 to 48 hours and the resulting larvæ feed for 3 or 4 days and then pupate. Some 4 or 5 days later the adult fly emerges, mates, and in from 12 to 24 hours the female begins to lay eggs. Thus the whole life cycle under suitable conditions of temperature and food is completed within 10 or 11 days. These flies are easily grown in a vessel containing banana pulp. The adults feed on the abundant yeast growth which appears and the larvæ burrow into and live on the pulp itself. A few flies placed in a "universe" consisting of a milk bottle properly provisioned will reproduce, grow old and die; their offspring do likewise until eventually a

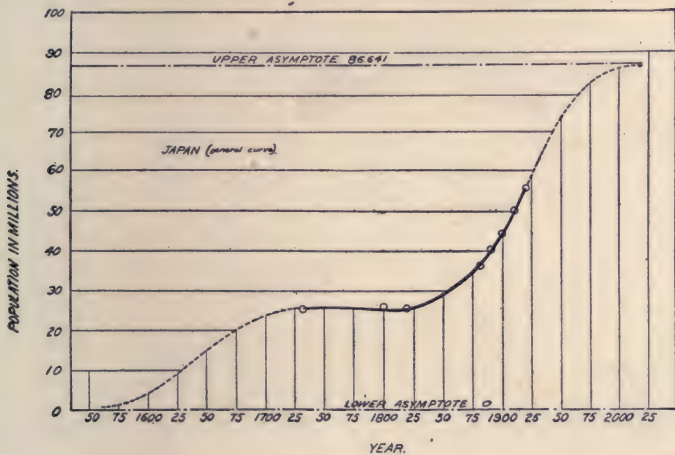


FIG. 96

The population growth of Japan. The upper limit of the present cycle of increase (upper asymptote) is set at 86,641,000. (From Pearl.)

dense population inhabits the jar. A census taken at short intervals shows, as indicated in the curve (Fig. 95), that increase at first is slow, then rapid, then slow again until it finally becomes stationary. And this is a fair prototype of other populations.

With man, whenever a new cultural state is entered upon, such as a shift from agriculture to industrialism, an irregularity in the curve appears but this merely means resuming the general cycle again on the new level. This is indicated in the diagram for Japan, Fig. 96, where there is a sharp upward sweep of the

curve coincident with a rather abrupt transition from one type of culture to another in the interval between 1825 and 1875.

The diagram for the United States (Fig. 97) shows its present population to have barely passed the stage represented by the rapidly ascending portion of the curve with a maximum population of 197,000,000 in sight about the year 2100. The curve of French population (Fig. 98), on the other hand, is already well beyond its period of rapid growth.

The curve for total world population (Fig. 99, p. 385) as nearly as it can be computed on the more reliable of the various estimates which have been made, fits the calculated values fairly

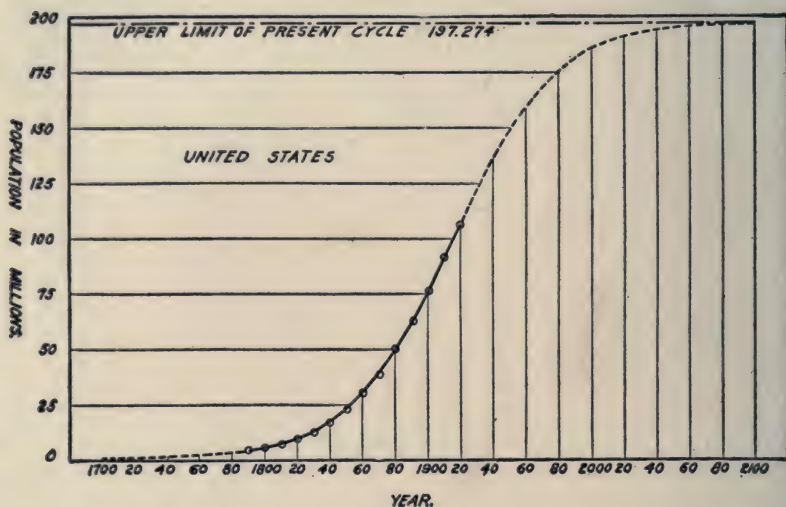


FIG. 97

The population growth of the United States. (From Pearl.)

well. Starting the present cycle of growth in world population in the sixteenth century with four hundred to four hundred fifty millions the rate of growth appears to have kept increasing up to 1869; since then it has been declining. According to Pearl's calculations the predicted upper limit of world population on the present basis of growth is somewhat over two billions and we shall be within six millions of reaching it by the year 2100. With our world population already set at seventeen hundred million we have only about three hundred million more to add,

or roughly, three times the present population of the United States. If a new growth cycle, conditioned by new factors, is to be entered upon before or at this time of equilibrium, it will have to be through means of food production beyond the present knowledge of science.

Law of Population Growth.—Pearl states his law of population growth as follows:

“Growth occurs in cycles. Within one and the same cycle, and in a spatially limited area or universe, growth in the first half of the cycle starts slowly but its rate per unit of time increases steadily until the mid-point of the cycle is reached.

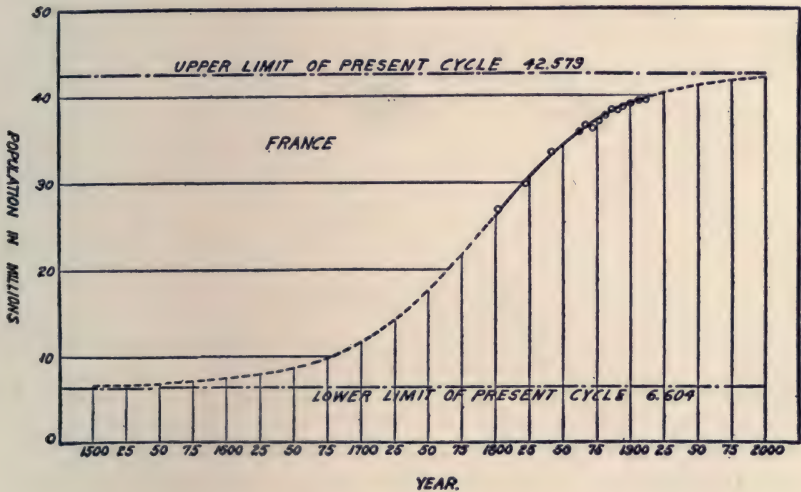


FIG. 98

The population growth of France. (From Pearl.)

At that point the rate of growth per unit of time is at a maximum. After the mid-point is passed the rate of growth per unit of time becomes increasingly slower until the end of the cycle. In a spatially limited universe the amount of increase which occurs in any particular unit of time, at any point of the single cycle of growth, is proportional to two things, viz.: (a) the absolute size already attained at the beginning of the unit interval under consideration, and (b) the amount still unused or unexploited in the given universe (or area) of actual and potential resources for the support of growth.”

The second factor, (b), would include discoveries yet to be made or resources still unused such as power, minerals or new agricultural regions, improvement in agricultural methods, development of better plants and animals, discovery of new and better food plants, the unlocking of new stores of energy, the possible chemical synthesis of foods, and improved transportation.

World Population and Food Supply.—In his *Mankind at the Crossroads* Professor East has brought together enough data on world population and world food-supply to give pause to even the most thoughtless individual. In one chapter he reviews item by item the suggestions of the credulous as to where the requisite new food is to come from and points out their underlying fallacies. At most he sees possibilities of adding not over 50 per cent. to the present world food supply.

In spite of the fact that since the war, for the American farmer at least, agricultural surplus rather than food shortage has been a pressing problem, this is but a passing incident in the race between population and agriculture. The temporary difficulty in finding profitable markets for farm products, due in part to the present impoverishment of food-purchasing nations, merely obscures the fundamental situation.

To any one familiar with the technical difficulties inherent in chemically constructing even the simplest of organic substances, the prospect of synthetic foods in any considerable quantities or with sufficient cheapness to make them widely available is not promising. As for the possibilities of discovering valuable new food plants East points out the significant fact that every important kind of food plant we have to-day was known and cultivated by prehistoric men. These include wheat, oats, corn, barley, rice and other grains, such legumes as beans, peas, lentils, and most of our present-day vegetables, fruits and nuts. There seems little prospect therefore of particularly valuable discoveries in this field. On the other hand the scientific breeder, through hybridization, the selection of useful variations and the perfection of high-yielding strains for different special conditions of soil and climate, will probably in time accomplish considerable crop increase, although some of the best informed authorities believe that an advance of 25 per cent. in productivity is the most that can be thus effected.

Intensive agriculture as practised in parts of Europe will

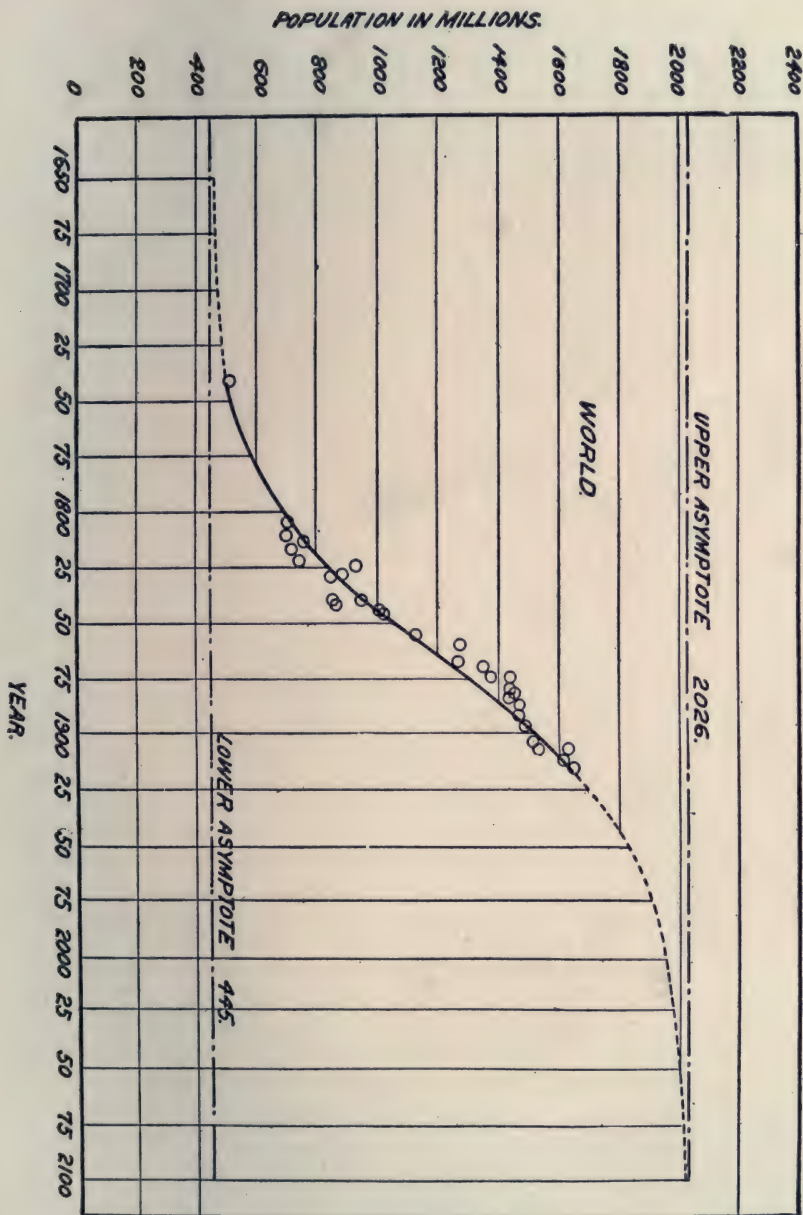


FIG. 99

The population growth of the world. The upper limit of the present cycle of increase (upper asymptote) is set at somewhat over two billions. (From Pearl.)

unquestionably increase crop yields, but in such regions doubling the yield over that of the United States is accomplished at a cost of five times the man-power. Sea foods can also be used more extensively, although this supply is by no means unlimited and already it requires more labor and money to secure a given amount of such food than formerly. Types of food plants more resistant to drought, to fungi or to insect pests will be developed, more efficient means of preventing the ravages of such enemies will be found, better methods of tillage and of crop rotation will be discovered, improvements will be made in methods of harvesting and marketing, and here and there other helpful increments will be secured, but at best these will postpone rather than avert the crisis.

Viewing the world country by country East finds that, very conservatively estimated, there is a total increase in world population of nearly twelve millions a year, or almost twice the total population of that Belgium we were striving to help feed a few years ago. Knibbs, a careful statistician, estimates the yearly increase at nearly twenty millions. We may safely say, then, that there are probably twelve to fifteen million more mouths to feed each year! How tremendous an acceleration in growth is in progress may be seen, as East points out, by considering certain aspects of our increase from the time of the first records of mankind on earth some 500,000 years ago. It took man till 1800 to reach a population of 850,000,000, but by 1900, just one hundred years later, this number had doubled. The present world population is 1,700,000,000 with a probable error of not over 40,000,000. At its existing rate of growth Knibbs estimates that this population would double in sixty-one years. Such a rate of increase, of course, will not, can not, go on for any considerable period of time. It must, as the saturation point is approached, gradually slow down. But what reasonable human being wants to see his nation reach a saturation point where probably personal comfort and advancement must be largely sacrificed because each person can have barely enough to sustain life?

After a detailed study of the world population and its growth, checked with the official census returns whenever such are available, East has tabulated the total world population as of 1916 by races, together with the annual rate of increase at that time and the number of years required for doubling the population of each race. This is set forth as follows:

Races	Population in millions	Annual increase per thousand	Annual increase in millions	Number of years to double
White, European origin	650	12.0	7.80	58
White, non-European ..	60	8.0	.48	87
Brown	420	2.5	1.05	278
Yellow	510	3.0	1.53	232
Black	110	5.0	.55	139
Total	1,750		11.41	

In all he finds ten hundred forty million in the colored races to seven hundred ten million whites. It will be seen that he does not agree with Stoddard's conclusion that the colored races are increasing much faster than the white. He finds, on the contrary, that exactly the reverse is true. He concludes that the rate of increase of whites of European origin per 1,000 is 12, instead of the 8.7 estimate of Stoddard. While recognizing how imperfect the census returns are in countries in which the colored races predominate he is convinced that their rate of increase has been greatly over-estimated. Because of the more reliable data available for the whites he has conservatively kept his estimate of their natural rate of increase at a minimal figure while computing the rate for the colored races at a maximal figure. From the table it is evident that even to-day the white race is more numerous than any of the other races. At present more than two-thirds of the total yearly increase in world population is white and if this race continues its remarkable rate of growth it will soon constitute an actual majority of the world population instead of a mere racial plurality. With a yearly increase of 8 millions of whites and only 4 millions of non-whites, the present ratio, East believes that, barring some unforeseen upheaval of world affairs, this majority will be attained before 1950. Even to-day the white race has political control of nine-tenths of the habitable globe and there is no prospect that it will relinquish this control as long as it can obtain food from the parts inhabited largely by colored races. If ever such territory becomes a liability instead of an asset it is likely to be fenced off by a white barrier and left to its own devices.

Rate of Increase in Representative Countries.—A glimpse at the rate of increase in representative countries is of interest. China with a population of some three hundred twenty-five to three hundred fifty millions seems to be approximately

stationary. Japan with a net increase of 13 per thousand shows a rising birth-rate and a stationary death-rate. India and the South Seas are sporadic and uncertain but may be estimated as having an average increase of about 8 per thousand. The blacks in America and the West Indies are increasing at the rate of 11 per thousand, in Africa more slowly, even showing a decrease in some regions. The countries of East Europe, such as Roumania, Bulgaria, Serbia and parts of Russia have a high birth-rate, as great as 40 to 50 per thousand, but since they also have a high death-rate the net increase is about 17 to 19 per thousand. It is interesting to contrast these last countries with Australia and New Zealand which have a low birth-rate, 26 to 28 per thousand, but which because of their low death-rate, also have a survival ratio of about 17 to 19 per thousand. In general a high birth-rate is accompanied by a high death-rate, a low birth-rate by a low death-rate, so that in spite of low birth-rates in such countries as Holland, New Zealand and Australia there is a rapid rate of natural increase. The one exception seems to be France. France has a low birth-rate but has failed to reduce correspondingly her death-rate.

Future Agricultural Possibilities of the World.—East's figures on the future agricultural possibilities of the world are also enlightening. He points out that there are probably about 13,000,000,000 acres of land on the earth available for food production. Allowing 2.5 acres as the minimum which will maintain each individual on the present dietary standard of the European peasant, the world can support 5,200,000,000, a population which at the present rate of increase would be reached in a little over one hundred years. This means that even the end of the present century, at this rate of increase, would see all the more inhabitable agricultural regions of the globe filled well toward the saturation point. Countries which can now export food would be kept busy supplying the home needs. Even to-day neither over-populated Europe nor Japan can wholly feed themselves. What will happen when they can no longer secure food from the outside?

When one scans the world at large the prospect is not reassuring. China, an agricultural country, is full with presumably a stationary population. North and Central Asia and even India can probably support a few more. The cultivable regions of Australia and New Zealand will soon be occupied. Africa and

South American can still support many although it remains to be seen if the white man can stand the tropical parts of these countries. The "friendly Arctic" looks promising to explorers usually in inverse ratio to their knowledge of agriculture. As for the omniscient newspaper paragraphers who from time to time magnanimously offer to get the whole world population within the boundaries of Texas, and feed it there through intensive cultivation, one could dismiss their patter along with the comic strips were it not that such false representation, innocent of any semblance of truth, seriously misleads many of their readers.

Available Farm Land in the United States.—Of the 1,903,000,000 acres of land in the United States, according to data published by O. E. Baker in the 1921 *Yearbook of the Department of Agriculture*, 503,000,000 acres, or 26.4 per cent. were in farms in 1920. Of these farm lands, however, only 375,432,000 acres, or about 74 per cent. were in crops. Of the 1,400,000,000 acres of unimproved land, after subtracting untillable land, such as deserts, forests, swamps, non-irrigable lands and areas occupied by cities, towns, roads and railways, Baker finds that only about 300,000,000 acres of new land which can be made usable through irrigation, drainage, clearing and dry farming, is left, and this in the main probably not as good as that at present under cultivation. This means that we can add about 60 per cent. to our present farm area. So, with anything like the present rate of increase, we shall not have to wait till a dim future for filling up. Our youngest children, or at least their children, will have to face the possibility of feeding 300,000,000; and yet, according to the estimates of both Pearl and East, in the United States 200,000,000 is approximately our saturation point.

Cheap Food Probably a Thing of the Past.—The inevitable conclusion would seem to be that cheap food is a thing of the past in the United States. The era of diminishing agricultural returns on the basis of less and less yield from a given amount of labor and of capital was entered upon somewhere between 1890 and 1900. Our present acreage planted to wheat, oats and corn is less per capita of population than it was in 1890 and all meat animals including milk cows are fewer per capita now than in 1880, 1890 or 1900. So we may well question with East whether it is a mere coincidence that following closely upon

the heels of this agricultural decline the trend of population in this country, in 1914, passed its point of maximum growth-rate as evidenced in Pearl's curve of population in the United States (Fig. 97, p. 382) and began to show progressive diminution. As this curve turns more sharply toward the horizontal we may expect to feel more and more acutely the effects of population pressure. America's "joy-riding" period of exploitation of virgin soils and other rich natural resources appears to be in sight of the end. Even at present we are importing more food materials than we export. Since it takes eight times more land to provide a man with a meat diet than with vegetable foods it is evident that in the not distant future the fatted calf, even in our own land, will no longer be the accustomed offering for the prodigal son because the fodder for its production will have long since gone to ease the hunger pangs of his overnumerous fellowmen.

With facts like these confronting us the futility of dreaming about the abolition of war, until the fundamental question of world population is settled, is evident. When the pangs of hunger cause a nation to begin to tighten its belt, it goes without saying, that nation is going to set forth to get food at any cost. Even defeat, with loss of millions of men, can be viewed with equanimity, since this relieves the pressure in the homeland. Some of the grim results of striving for "a place in the sun" have only too recently been before us to require comment.

Key Commodities and International Disputes.—Directly or indirectly the subject of most international disputes to-day is that of various key commodities such as iron, oil, coal, copper, wheat, cotton and the like. While at first sight some of these, notably the minerals, may seem far removed from the problem of population and food supply, in reality they merely present other aspects of this problem. Thoughtful statesmen everywhere are rapidly rousing to the importance of having more accurate knowledge of the world's mineral resources, since free access to such supplies is unquestionably the chief guarantee of the peace and prosperity of most modern nations. Adequate sources of the minerals most in demand are few, hence, according to Professor C. K. Leith, who was chief of the minerals division of the commission to negotiate peace at the conclusion of the late World War, the political control of mineral resources means the control of the world. Since the United States contains about eighty per cent. of the world's natural resources which are

required in case of war, the question is by no means an academic one for the American citizen. In a recent article in *Foreign Affairs*, Professor Leith makes the significant statement: "England and the United States alone, by agreeing on the disposition of the mineral supplies they control, are in position to determine the general course of the mineral industry of the world." Since a modern war can not be waged without unlimited supplies of iron, steel and coal, a war of any considerable magnitude with such a nation as Japan, for example, Professor Leith regards as an idle dream because Japan lacks available iron ore and fuel. His predictions made in 1918 as to what the inevitable outcome of the Ruhr situation must be, based on the economic necessities of the case, have largely been fulfilled, and his opinion therefore is one which should carry much weight. He argued that the coal of the German region and the iron of the adjacent French territory must be brought together into reciprocal working relations, or both countries must suffer economic disaster. In other words the economic necessities of the case must in the end override all considerations of national boundaries, and such is rapidly proving to be the case. So too, according to Professor Leith, other economic units, irrespective of political boundaries must inevitably be established. All of which means, in other words, that there are increasing numbers of hungry mouths to be fed and no conventionally established boundaries can withstand the inexorable drive for food.

Criticism of American Birth-Rate Statistics.—And yet let us not overlook other possibilities of the case. Louis I. Dublin, chief statistician of the Metropolitan Life Insurance Company, in a recent article in the *Atlantic Monthly*, maintains that we in America are far from where the quantity of our population need give us concern. He cites the facts that we are supporting only 90 persons per square mile of land as against France's 200 persons per square mile and that yet France is not over-populated. He tells us nothing, however, about how much of France's food, compared with ours, is home-grown and how much of it is obtained through exchange of manufactured goods in other lands, nor does he inform us that to double our productivity per acre as is now done in some parts of Europe requires five times the man power, and he makes no comments on how this may affect our standards of living.

Dublin thinks the prevailing methods of computing natural

increase on the gross birth-rates and death-rates are faulty and have misled us. He believes that our natural annual increase, usually set at 11 per thousand, is in fact not nearly this high. He makes the point that as the result of the higher birth-rates of past generations in the United States there is at present a disproportionately large number of persons at the reproductive age of life, and that the current birth-rate in consequence is swollen beyond what it should be. Making the necessary mathematical correction on the basis of a normal age distribution reduces the birth-rate from 23.4 per thousand, the present figure, to 20.9 as the true measure of our reproductive activity. Furthermore, a second result of this overplus of descendants of a more fertile generation is to reduce the death-rate disproportionately since death-rates are at their lowest in early adult life. Making the corresponding correction for this end of the score the annual death-rate would become 15.3 per thousand instead of the present 12.4. When these two corrections are made Dublin finds that the annual rate of net increase per thousand is not 11 but 5.5. If one goes still further and reckons with the effects of recent diminution in mortality rates, the rate of natural increase becomes still lower—as low as 3.6 per thousand when figured on the basis of our present procreation rate and the mortality rate of 1910.

Assuming that these corrections are valid, as they probably are for the period concerned, it is difficult to appraise their full significance. When a population approaches a state of equilibrium it is uncertain whether the occasion should be one for rejoicing or for fear. Dublin himself evidently regards it as dangerous. If, however, to use his own phrase, a “well-organized and happy society” should be our aim, then the important thing is not to go heedlessly on to the saturation point set by population pressure but to strike a balance at the level of maximum efficiency and comfort.

Improved Machinery and Future Food Supply.—As one reviews the estimates of various statisticians on future food supplies, the most outstanding omission from their calculations seems to be the part improved machinery may play in future production. A few men with suitable machines can now accomplish what formerly required the efforts of scores of laborers, and there is every reason to believe that further vast extensions of manpower will be thus secured. While machinery and invention can

not restore fertility directly to heavily-cropped soil, it can accomplish the same thing indirectly by cheapening the production of artificial fertilizers, and it can make it practicable to farm land that could not be cultivated profitably by direct hand labor. How far this can postpone the saturation point is, of course, uncertain, and what mitigation of the possible evils of saturation, if any, it will provide, is even more problematical. It will mean, for a time at least, fewer required hours of human labor and more leisure for the individual, but whether this will be a curse or a blessing—whether such leisure will be used for culture, vice or war—remains to be seen. Such easement might result merely in renewed reproductivity of those individuals relieved from drudgery, and a consequent hastening of the time of population repletion. This much is sure: whatever machinery may do, it can not extend the earth's surface, so that even with its aid man, with an unchecked natural increase in numbers, must eventually reach a condition of stalemate.

Dangers in Complex Social Organizations.—As our civilization commits itself more and more to the intricacies of interlocking specializations and becomes in effect a huge machine, it is at the same time putting itself at the mercy of any of its parts, even the most unreliable. If we become increasingly the slave of the machine may not our civilization perish by the machine? Already society has become so complex that a slip anywhere in its organization, be it but the revolt of a handful of transportation operatives or of coal miners, means widespread disorder. That fraction of one per cent. of our inhabitants which constitutes the brains of our industrial and research laboratories, even now could hold the welfare of modern civilization in the hollow of its hand if it chose to unite and dictate world policy. How far could we get in either war or peace under existing conditions without the skilled hand, the seeing eye, the understanding, creative mind, of the inventor or the scientist back of our daily occupations, or of even many of our most trivial doings? If the scientists and technologists of the world would stand together and say "no," what nation could wage war?

Truly social and industrial conditions are rapidly coming to exemplify the Biblical maxim, "Ye are parts one of another. . . . For none of us liveth unto himself and no man dieth to himself." Will the giant organism known as civilization, like the grotesque

monsters of Mesozoic times, go to its final extinction because of its very hugeness and intricacy? Who knows? This alone we can affirm: With the dependence of one upon another to which we are becoming more and more committed, serious disruptions of our system become increasingly probable and increasingly hazardous.

On the other hand, to escape undue "crape-hanging," one may seek a brighter side of the picture. Perhaps, as population pressure reaches the point where human comfort is seriously threatened, the marked capacity of all living things for adaptation to new conditions as they arise may come to the rescue in human society, and man will adjust by an altered birth-rate or by discovery of new means of subsistence, or both. If man will use the intelligence with which he is provided, it surely is possible to strike an equilibrium in world population far short of misery for all mankind.

General Increase in World Population Is Undesirable.—

There can be no question that we need more light on the whole problem of population. It is a highly complex one with many technical factors involved, and we are not yet in position to arrive at final judgment. Nevertheless various broad aspects of the question seem clear. If anything is obvious it is that the world is not in need of a general increase in population. To the militarist, of course, the more people there are in a nation the more killers there will be to slay the inhabitants of some neighboring nation. Their ideal is that of Napoleon who pronounced that woman greatest "who furnishes the most cannon-food at her country's need." And yet it is permissible to inquire if, after all, the human race is so absolutely stupid that it can learn by no other means than slaughter, rapine and destruction.

The only serious feature of our national declining birth-rate is its selective nature. It is the superior types which are declining while the inferior are coming to outnumber them more and more. The *quality* of our population should concern us far more at present than its *quantity*. Moreover, because they respond more quickly to a change in economic conditions, the higher classes are the first to show a decline in birth-rate with the coming of economic hardship. Yet, we can not advocate that our better stocks enter into a breeding competition with the mediocre and inferior. The most we can legitimately demand of them is that they maintain themselves.

To-day in our own country we are witnessing the passing of power largely from the hands of the older white American stock and its concentration for good or ill in those of recent aliens. The decline of a nation is a function of the loss of certain qualities possessed by its leaders, indeed, the loss of its leaders. Suppose the abler one-tenth of America were exterminated to-day, where should we be? And we should remember that capacity for leadership is largely an inborn, not an acquired, characteristic.

What's the answer? Whether we have the answer or not, all thinking people will agree that one must eventually be found. Apparently sooner or later mankind must choose between reduction of standards of living and restriction of population. Medical research seems to hold out promise of an ultimate annual death-rate of as low as sixteen per thousand, hence a birth-rate of sixteen per thousand also will be all that is necessary to maintain a people. The present birth-rate, according to the best figures available for the world at large, is in excess of this by at least nine per thousand of general population.

Thus taking the world as a whole the average birth-rate is too high for safety. The ultimate check to any population whether it be that of lower animals or of man is lack of food. It is the old story: population tends to increase in multiplicative ratio; food not so rapidly. The final stark question is that of food, and who shall eat it? If man is not intelligent enough to take his own evolution in hand and keep it within the limits of his food supply, then nature will do it for him in the same old crude, ruthless way; war, famine, and pestilence will become the final arbiters.

CHAPTER XXII

IMMIGRATION

We hear much in these days about the economic and immediate social problems of immigration. But important as these undeniably are, they are probably insignificant compared with the biological problem involved. It seems never to occur to most of us that sooner or later, in a few generations at most, we must drink the blood of this stock into our own veins through interbreeding.

Democracy, a Biological Problem.—It is evident that what our democracy will be depends in large measure on the natural abilities and inclinations of ourselves and of our fellow-countrymen. The main problem, indeed, becomes largely one of who our fellow-countrymen are, since because of numerical superiority their wills must in large measure prevail. As long as they are of the same race or stock as we are, opinions will doubtless be fairly harmonious, ideals much the same. But the standards of a different race or stock are likely to differ from ours. Our present institutions, social, political, religious, are largely north European in origin. The precious things for which our American government stands, peace, justice, honesty, protection of life and property, personal freedom, are but the embodiment of the united wills of the individuals who have made our nation.

The intellectual, moral and spiritual characteristics which constitute the source of a nation's social institutions and government are in the main but the outward expression of the strong inherent trend that is a part of the very being of the people of that nation. Change its racial stock and inevitably its institutions must change. Free institutions are but the expressions of free men, and the spirit which makes and keeps men free is largely inborn. Initiative, courage, reliability, enterprise, high ideals, and creative imagination on the part of the individual citizen will inevitably be expressed in the institutions created by such citizens; and the roots of all these qualities are innate. "By their fruits ye shall know them." The lethargy of the dullard will never kindle into a glow from the flaming torch of freedom. The frenzy of if

the fanatic will never lend itself to the establishment of that dispassionate justice which is our ideal. The lawless spirit of anarchy can never express itself in peaceful pursuits and orderly institutions. So, does it not behoove us to scan with anxious eye our citizenry to see what we are doing to insure worthy heirship to our heritage of democracy? Are these benefits to accrue to the descendants of the original stocks which colonized America and made the United States what it is at its best, or are they to be for alien blood? If the latter, then how sure are we that our institutions will continue to exist?

Native- and Foreign-Born.—Most of us, indeed, little realize how much of the population of the United States to-day is made up of people of foreign birth or of the immediate children of the foreign-born. According to the census of 1920 there were 13,712,154 foreign-born white individuals in the United States; that is, one out of every seven or eight inhabitants. But, if to the foreign-born we add those with one or both parents foreign-born, the total rises to 36,398,958 or approximately one-third of our entire population. During the decade 1900-1910, 8,500,000 foreigners came to the United States, of whom some 5,250,000 remained to make a permanent home. In the following decade, in spite of the check due to the World War, more than 6,000,000 immigrants arrived. The estimate is that in general four-fifths of the immigrants remain permanently. During the first three-fourths of the nineteenth century immigration, on the whole, probably strengthened America, since it was made up of energetic, progressive individuals belonging to races closely allied to the original colonists. Later, however, there followed a deluge which unquestionably was not up to the average of its own country. Not only are certain of our later immigrants apparently incapable of understanding our institutions and our ideals, but with their lower wages and low standards of living they become serious competitors to workmen of our own blood. The earlier immigration was independent; the later, largely dependent.

Comparison of Natural Increase with Immigration.—With a total population of over five and a half million, three-fourths of the inhabitants of New York City are of non-English speaking people. In his *American Police Systems* Fosdick points out that the white population of native parentage constitutes less than one-fifth of the total population of New York City; less than one-fourth the population of Chicago, Boston, Cleveland, Detroit,

and Milwaukee; and little more than one-tenth that of Fall River, Massachusetts. In only fourteen of the fifty largest cities of America does the native population constitute half of the total!

When the state of New York had 9,000,000 inhabitants among them were found 840,000 Russians and Finns (the Russian being mostly Russian Jews); 1,000,000 Germans; 470,000 Austro-Hungarians; 125,000 Canadians (mostly French-Canadians); 720,000 Italians; 880,000 Irish; 310,000 British, and 90,000 Scandinavians.

In a single ward in the city of St. Louis Fosdick found 2,301 foreign-born Germans; 2,527 foreign-born Italians; 7,534 foreign-born Russians; 900 Austro-Hungarians; 495 foreign-born Roumanians; and 14,067 others of foreign parentage, as well as 1,602 negroes. Surely such figures as these must drive home to us the magnitude of our immigration problem!

The rapid and steady increase in population of the United States during the past half-century has been due largely to immigration and the high fecundity of the immigrant woman, rather than to the productivity of native stock. For instance, the births in the state of New York in 1912 were a few over 216,000, but the number of immigrants settling in New York that same year was over 239,000. Moreover, the foreign family, as nearly as can be estimated, outbreeds the native family in the ratio of at least five to three. Arriving during their reproductive years immigrants commonly produce large numbers of children. There is evidence, however, that their families tend to become smaller in successive generations in the United States. A critical analysis of American population statistics by Professor Wilcox shows that a decline in the native American birth-rate, began and has continued from as early as 1810. The situation has been obscured partly by our diminishing death-rate and partly by the effects of immigration.

Is the Contribution a Desirable One?—The importance of immigration to our democracy, of course, hinges on whether or not the contribution we are receiving is a desirable one. It takes but a glance at available statistics to see that much we have been receiving in recent years is wholly undesirable. We find that in one year (1908) at Ellis Island alone, 3,741 paupers, 2,900 persons with contagious disease, 184 insane, 121 feeble-minded, 136 criminals, 124 prostitutes and 65 idiots were denied entrance, and yet, according to the estimate of Doctor F. K.

Sprague, of the United States Public Health Service, probably only about 5 per cent. of the mentally deficient and 25 per cent. of those who would become insane were detected. When confronted by such data we can begin to realize what we are facing. Others estimate that from 6 to 7 per cent. of the immigrants who were arriving before the war were feeble-minded. We learn further that recently while the foreign-born population of New York State was about 30 per cent., the foreign-born population of the insane hospitals of the state was over 43 per cent., and at one time approximately 65 per cent. for New York City. In one year (1908) 84 per cent. of the patients in Bellevue Hospital, New York City, were of foreign parentage. Paresis, which probably always has syphilis as its antecedent, is proportionately twice as prevalent among foreigners as among natives in New York City. From a special report on the insane and feeble-minded in the United States, based on the census of 1910, we find that while foreign-born whites constituted 14.5 per cent. of the total population, they made up 28.8 per cent. of the total number of inmates in our asylums for the insane.

In passing, it may be remarked that the American people can find abundant food for thought in observing how their immigration laws have been enforced—or not enforced—in the not distant past. At one of our ports in 1910, of 1,483 immigrants certified as unfit to land because of serious mental or physical defects, 1,370 were landed nevertheless, and at the port of Boston in November, 1910, of 250 immigrants certified by the medical corps for major defects, all but *three* were given entrance!

Recently, for the Congressional Committee on Immigration, Dr. H. H. Laughlin of the Eugenical Record Office examined 210,855 inmates in 445 of our 667 state and federal custodial institutions with reference to such conditions as feeble-mindedness, insanity, epilepsy, crime, tuberculosis, blindness, deafness, deformity, and pauperism or dependence on the community. Taking all defects together, he found that the foreign-born showed almost double the proportion yielded by the native-born of native parents; that while the foreign-born made up 14.70 per cent. of our total population they constituted 20.63 per cent. of the inmates of our jails, almshouses, and institutions housing the insane, feeble-minded, epileptic, chronically diseased, crippled and deformed. While it is clear that to make a fair

comparison with similar conditions among individuals of native parentage, certain corrections should be made such as the possibility that foreigners are more likely than natives to be placed in state and federal custodial institutions, that there are relatively more adults among the foreigners, that environmental pressure is more severe for them, and the like, nevertheless, with all possible corrections made, the facts are far from reassuring.

Dr. Laughlin compared the number of individuals in each racial group found in these institutions with the total number of the same group found in the population of the United States. A group which furnished such inmates in the same proportion that it furnished inhabitants to the United States was said to fulfill its quota by 100 per cent. In such a comparison some very instructive facts are brought to light. Thus, in insanity, Ireland leads with a percentage of 305, that is, over three times its legitimate allowance; Russia is second with 266 per cent.; and Scandinavia third with a percentage of 193; while whites of native parentage constitute 73 per cent. In crime the three highest in percentages are the Balkans with 278; Italy, 218; and Russia, 126, as compared with a native quota of 82. For dependency the score reads: Ireland 634; Great Britain 218, the Balkans 121, native 104; for epilepsy: Great Britain 146, Russia 117, Ireland 108, native 93; for tuberculosis: the Balkans 379, Scandinavia 214, Russia 200, native 89. When it comes to feeble-mindedness, deformities, deafness, and blindness, the native whites of native parentage would seem to be inferior to the foreign-born, but this is probably due to the fact that such conditions are more easily detected in individuals beyond the age of young children and that such immigrants have been excluded under our laws. This supposition is borne out by the fact that among children of immigrants these defects show a disproportionate increase.

We have not space to review this study* in detail, but there are certain outstanding facts that should be mentioned. Taking defectiveness as a whole, Ireland stands first, with a quota fulfillment of 209 per cent.; Russia-Finland, second, with a quota of

* See:

1. Analysis of America's Modern Melting Pot. Hearing before the Committee on Immigration and Naturalization, House of Representatives, Sixty-Seventh Congress. Third Session. Serial 7-C. Pages 725-831. Washington, 1923.

2. Jennings, H. S., "Undesirable Aliens," *The Survey*, Dec. 15, 1923.

184 per cent.; and the Balkans third, with 175 per cent. Thus the problem can not be resolved into a question of Northern and Northwestern Europe versus Southern and Southeastern Europe as has been commonly supposed. The country with the worst record, Ireland, lies in the north and west division of Europe; that with the best record, the present Czecho-Slovakia, and part of Jugoslavia and Poland, in the south and east division. The north and west division has the worst record for insanity and dependency; the south and east for crime, feeble-mindedness, epilepsy and tuberculosis. No one country has a monopoly of all defects.

It is obviously impossible, therefore, to keep out undesirable European aliens by rejecting immigrants on a basis of race or nationality. The only satisfactory outcome can be reached by careful selection of the immigrant in the land of his origin, and not only the individual but the family of which he comes must also be taken into consideration.

Intelligence Rating of Foreign Stocks.—However great, from the standpoint of inheritance, the danger may be from classifiable defectives, it is probably greater from that larger class of aliens we have been receiving with open arms who are below the mental and physical average of their own countries. Even with the best of inspection it is well-nigh impossible to detect the grades of feeble-mindedness above idiocy and imbecility in the great numbers of foreign children under five when brought in.

The army intelligence rating (page 358), which was applied to conscripts during the late war, also, in so far as it is valid, sheds a flood of light upon the quality of much of the foreign-born population of the United States. The tests for foreigners were not conducted in English but in their own tongue. While in the white draft as a whole 22 per cent. were found to be of inferior intelligence, the percentage rose to 46 for the foreign-born when grouped apart from the others. The peoples of different nationalities differed somewhat. Thus, of those of Polish birth 70 per cent. ranked as of inferior intelligence; of Italian birth, 63 per cent.; of Russian birth, 60 per cent. Of our negro troops, 89 per cent. rated under the mental age of thirteen. An almost negligible number of individuals of superior intelligence were found among the foreign-born.

The results from the army tests of alien conscripts when used

as an index for rating the intelligence of our total foreign-born population gives the following significant classifications:

		Per cent.
Very superior	153,128	1.1
Superior	403,700	2.9
High average	1,016,211	7.3
Average	3,702,904	26.6
Low average	2,206,914	16.5
Inferior	4,287,573	30.8
Very inferior	2,060,262	14.8

According to these figures, 6,347,835 aliens—nearly half our total foreign-born population—are classifiable as of inferior intelligence. Since the fate of a democracy must be determined by the intelligence of its voters one may well raise the question of how wise we are in opening citizenship to aliens as readily as we do.

Percentage of Crime in Immigrant Stock.—Again, according to Fosdick, there is a direct connection between the presence of foreign races in America and crime. In our large cities the percentage of arrests of foreigners is in excess of their relative proportion of the population, and not merely for misdemeanors which might be due to ignorance of minor police regulations, but for serious crimes, such as assault, burglary and murder. In 1918, for example, the Irish-born inhabitants of Boston constituted 9.8 per cent. of the inhabitants but they represented 15 per cent. of the total arrests for crime. In 1917, representing 10.15 per cent. of the population of New York City, the Russian-born inhabitants composed 20 per cent. of the arrests, and in the same year the Italian-born inhabitants of New York City, although constituting only 7.15 per cent. of the population, showed 11.8 per cent. of arrests for crime. Of 148 foreign-born charged with homicide in New York City in 1915, 65 were born in Italy and 12 more were of Italian parentage. We find reports that crime has greatly diminished in certain communities in Italy, and an American commission which was investigating the matter was told that it was because the criminals had gone to America!

The following tabulation of arrests for felonies as distinct from the less serious misdemeanors, taken from Fosdick's *American Police Systems*, illustrates the situation in Chicago in 1918:

Country of Origin	Percentage of total population	Percentage of total felony arrests
U. S. white	62.1	55.1
U. S. colored	2.0	13.2
Poland	5.8	6.4
Russia	5.6	5.9
Italy	2.06	4.3
Germany	8.3	2.4
Lithuania (including Letts)9	2.3
Other nationalities	12.+	10.+

Legislation.—A new flood of immigration started immediately after the war but fortunately it has been materially checked by our recent legislative enactments, notably the general Immigration Act of 1917 and the Act of 1924. The latter attempts to fix quotas for different countries in such a way as to keep the bulk of the new aliens of the same racial white stocks as those which originally peopled the country and established its institutions. This is accomplished by limiting the number of immigrants admitted yearly from each European country to two per cent. of the number of foreign born from that country who were residents of the United States at the time of the 1890 census. Since there were relatively fewer southeastern Europeans here in 1890 than in 1910 the law favors immigration from northwestern Europe. While the numerical limitation accomplished by the law is an important gain it may be questioned if, so long as the applicant is white, more insistence upon good mental, moral and physical standards and less upon place of birth is not desirable.

Since the restriction is in effect, the problem of smuggling in of aliens across the Canadian and Mexican borders and from the seacoast has become a serious one. According to the estimates of Secretary of Labor Davis, more than 100 are smuggled in daily through our ports or over our land borders. At from twenty to forty dollars a head, and in the case of Asiatics sometimes even much higher, it is easy to see how lucrative this illicit business has become. It is evident also that the quality of the immigrant brought in by such means is likely to be of the lowest.

There is good reason to believe, furthermore, that certain countries are deliberately trying to use the United States as a

dumping ground for their undesirables while urging the best of their citizens who already have immigrated to this country to return home. The worst offender in this respect is the loudest protestant when it is suggested that we inspect and select our immigrants in the country of their origin. And yet this is the obvious way of preventing the hardships which may occur if rejection is left until the alien reaches our port of entry.

Under the new law, however, a consular officer may refuse to issue an immigration visa if he has reason to believe that an immigrant is inadmissible to the United States, so that a reasonably efficient consul can thus exclude many undesirables. Since certificates are good for four months and are issued only up to the numbers allowed by the quotas, the former rush at the beginning of each month and at the end of the year is done away with and this permits of more deliberate and thorough medical inspection at American ports. As a matter of fact inspectors and physicians should be present on all immigrant-carrying vessels so that the aliens could not only be examined thoroughly but kept under observation for several days. The authorization for such a procedure is already embodied in the Act of 1917 but our Government seems never to have taken any action in the matter. The clauses of the Act of 1924 which prohibit the landing of alien seamen who are excludable under our immigration law, and which increase the fines on transportation companies for bringing inadmissible immigrants, are also helpful.

Importance of Registration.—The best means suggested for preventing the surreptitious entrance of immigrants seems to be the plan of registration advocated by Secretary Davis according to which every alien would be required to register and enroll annually. Most of us do not protest at having to carry an annual automobile registration card or even a golf-club card which must be shown upon demand to the proper authorities and there seems no valid reason why candidates who are obtaining the favor of residence in this country should find such a regulation an undue hardship. No alien who is rightly here can object and the ones who enter illegally can be promptly detected and deported.

The United States is the largest immigrant receiving nation in the world, and the question of what immigrants should be admitted is one for it alone to determine. It is certainly high time that we give this whole question of immigration the most

serious consideration of which we are capable. Through the yearly quota under our present restriction law is only 164,667, consular reports reveal that more than a million and a half peasants and workers—mostly from the countries of eastern and southern Europe—are seeking admission as immigrants. Since, sooner or later, we must inevitably mingle our life blood with that of such invading hordes, or possibly be replaced by them, our very existence as a nation is at stake.

We may well ponder the evidence presented by Thomson in his "Standards of Living as They Affect Competing Population Groups" (*Science Monthly*, July, 1923) to the effect that: "When groups of people (races, nationalities, classes) having different standards of living come into competition, that group having the lower standards tends to displace and supplant the group or groups having higher standards."

It remains for us as a people to decide whether we shall continue to leave the determination of the character of our future population to foreign countries, to the large employers of cheap labor, to the railroad and steamship agents and brokers, or to sentimentalists or interested organizations who care nothing about the inborn fitness of the immigrants they bring, or whether we shall insist upon a proper regulation of this flood, so that we may receive only an honest, intelligent, industrious stock capable of understanding and upholding our laws and institutions. To continue to absorb these aliens with as little selection as we have done in the past is nothing short of criminal carelessness.

Cross-Breeding of Races.—Aside from the dangers which lie in the assimilation of foreign peoples of low native intelligence and the defective or unsuccessful types already discussed, some students of heredity feel that there is great hazard in the mongrelizing of distinctly unrelated races. Others, however, see no danger in inter-racial marriage. The fact is that cross-breeding of human races has not been studied with sufficient care to permit of a reliable judgment. At best we have little more than a series of opinions not one of which is based on unassailable grounds. In many of these, sentiment rather than fact rules. In the first place anthropologists do not agree upon the classification of the human races nor even upon the distinguishing features which shall be selected as a basis of classification. Such distinctions as skin-color (white, brown, yellow, red, black), hair-form (kinky, wavy, straight), body-build, stature, form of skull,

shape of face, characteristics of nose or cheek-bones, eye-form, thickness of lips, and body hair are all used in such classifications but there is no consensus of opinion upon the relative significance of these features. The fact that several of them are now believed to be bound up more or less intimately with endocrine secretions greatly complicates the situation. Thus the removal of a stock to a new territory with different environmental influences might result in modifications of various of the characteristics mentioned. Thyroid secretion, for example, apparently profoundly modifies many bodily features, and since the function of the thyroid is influenced by substances containing iodine, a difference in the iodine content of the drinking water or the food might result in a corresponding modification of certain structural or even mental characters.

The term *race* is itself a rather uncertain one when applied to human beings. To the geneticist a pure "race" would be one descended without admixture from a single pair of ancestors. As regards man the evidence is not unequivocal, even, that present mankind as a whole is derived from a single source. Genetically considered races are distinctive in the degree they differ in numbers of characteristics. When it comes to human beings about all we can say is that a race is a more or less pure-bred group of individuals who are much alike because of common ancestry. It is questionable if there is any "pure race" of human beings to-day; all we are justified in asserting is that there are more or less distinctive types. Extensive migrations with subsequent blood mixtures have been going on for ages, probably ever since neolithic times, if not earlier, in Europe. Such so-called "races" as the French or the Anglo-Saxon are highly composite, and the American is even more so. In Africa various of the negroid stocks are shot through and through with Arab blood and the Mongolian or Malay or Indian "races" are no less mixed. Most of the distinctive characters in races are compound and the underlying factors are usually brought together in the racial hybrid in such a way as to produce the impression of a blend; thus, while in certain simple characters such as eye-color, Mendelian alternative inheritance is in evidence, in general the hybrid offspring is intermediate between the parent races.

Dr. Hooten, after a study of the effect of race mixture on physical characters, concludes (*Scientific Papers of the Second*

International Congress of Eugenics) that: "It seems probable that in case of race mixtures morphological features are inherited by the offspring in small units from both parent stocks." While recognizing the lack of a sufficient body of evidence fully to substantiate such a conclusion, he is inclined to believe that the teeth of negroid types are characterized by certain peculiarities of form and a condition of the enamel which usually gives them a bluish or yellowish tinge, and that these negroid features persist in negro-white mixtures. He asserts that the form and proportions of the nasal bridge and nasal aperture are hereditary. He points out that negroid or mongoloid races are characterized by a primitive low and broad nasal bridge and says that hybrids between such a race and a race with high narrow nasal bridge usually approximate the latter nasal form. According to Hooten elevation of the nasal bridge is generally the most striking effect noticeable in a cross between a European and a low-nosed race, although he goes on to say that the primitively broad nasal apertures seem to be less readily affected by such crossings. He pronounces the protrusion of the jaws known as prognathism, a simian reminiscence, and finds that crossing of prognathous and orthognathous (short-jawed) races invariably result in a shortening or sometimes in a complete disappearance of this jaw-protrusion in the hybrid. Even a small admixture of the blood of a short-jawed race tends greatly to lessen negro prognathism.

In most primitive, hard chewing peoples, such as the Eskimo, he finds an increased palatal area, brought about by enlargement of palatal breadth. He regards the extreme specialization of the masticatory apparatus as being an important determining factor in the head form of such a type as the Eskimo which is characterized by a long, narrow, and high cranium.

Considerable interest has arisen lately in the question of whether or not pronounced racial intermixtures such as we have here in America may not result in such disharmonies of parts as to constitute a serious physiologic evil in many of the progeny of such crosses. Since it is impossible to settle the question on the basis of our present knowledge, it is not surprising to find widely differing opinions, even between men of high standing in genetics. Thus we find Davenport, Director of the Station for Experimental Evolution at Cold Spring Harbor, New York, in an article on "The Effects of Race Intermingling" (*Proceedings*

of the American Philosophical Society, 1917), although warning us that the subject has not been sufficiently investigated, making the following statement:

"Turning to man, we have races of large tall men, like the Scotch, which are long-lived and whose internal organs are well adapted to care for the large frames. In the South Italians, on the other hand, we have small short bodies, but these, too, have well-adjusted viscera. But the hybrids of these or similar two races may be expected to yield, in the second generation, besides the parental types also children with large frame and inadequate viscera—children of whom it is said every inch over 5' 10" is an inch of danger; children of insufficient circulation. On the other hand, there may appear children of short stature with too large circulatory apparatus. Despite the great capacity that the body has for self-adjustment it fails to overcome the bad hereditary combinations.

"Again it seems probable, as dentists with whom I have spoken on the subject agree, that many cases of overcrowding or wide separation of teeth are due to a lack of harmony between size of jaw and size of teeth—probably due to a union of a large-jawed, large-toothed race and a small-jawed, small-toothed race. Nothing is more striking than the regular dental arcades commonly seen in the skulls of inbred native races and the irregular dentations of many children of the tremendously hybridized American.

"Not only physical but also mental and temperamental incompatibilities may be a consequence of hybridization. For example, one often sees in mulattoes an ambition and push combined with intellectual inadequacy which makes the unhappy hybrid dissatisfied with his lot and a nuisance to others.

"To sum up, then, miscegenation commonly spells disharmony—disharmony of physical, mental and temperamental qualities and this means also disharmony with environment. A hybridized people are a badly put together people and a dissatisfied, restless, ineffective people. One wonders how much of the exceptionally high death-rate in middle life in this country is due to such bodily maladjustments; and how much of our crime and insanity is due to mental and temperamental friction."

Davenport was led to his conclusion, in part at least, from certain results he obtained by crossing Brahma and Leghorn fowls. The Brahma becomes broody two or three times a year and makes a good mother, but is only a fair layer. The Leghorn, on the contrary, is a poor mother but an excellent layer. "The

hybrid," says Davenport, "was a failure both as egg layer and as a brooder of chicks. The instincts of the hybrids were not harmoniously adjusted to each other."

On the other hand, Professor Castle, geneticist at the Bussey Institution of Harvard University, sees no danger in mixed races. He says:

"Crosses made between the largest and smallest known races of rabbits, one weighing three times as much as the other, produced cross-breeds which were remarkably vigorous and prolific, intermediate in size between the two parent races, and later generations showed no return to original size of the pure parent races. The inheritance of size depends on factors which are general, affecting all parts of the body. A rabbit of large weight also had long skull, long ears and long leg bones to match the great weight, and a rabbit with short ears was invariably of small general size. We may dismiss as groundless the fear that a mixed human race will necessarily contain physical features of unbalanced proportions. As a matter of fact, some of the best human stocks have arisen as race mixtures. The tall Scotch, and the short stocky Welsh are relatively unmixed ingredients of the intermediate but not less successful English type."

Professor Castle clearly inclines to the view that the more variable population which results from racial admixtures, at least where the stocks are not widely dissimilar, is more adaptable to a new or changing environment either physical or social and he suggests the possibility that the racially mixed nature of the populations of such countries as France, Germany, England and the United States has been an important factor in their adaptability to social and economic changes.

As far as our present knowledge goes, then, there seems little reason to fear crosses within the white race, provided the individuals concerned are of good quality. A not uncommon point of view among students of the problem is that races far removed from each other in physical characters and constitution, or which live under very different climatic conditions, are likely to prove unfavorable while beneficial effects are likely to arise from crosses between related races. Here again conclusive proof is lacking.

The mulatto in our own country, the Eurasians in India and the mixed races of South America are, according to the testimony of some observers, eloquent arguments against such hybridization. Agassiz remarked on this point:

"Let any one who doubts the evil of the mixture of races and who is inclined from mistaken philanthropy to break down all barriers between them come to Brazil. He can not deny the deterioration consequent upon the amalgamation of races, more wide-spread here than in any other country in the world, and which is rapidly effacing the best qualities of the white man, the Indian, and the Negro, leaving a mongrel nondescript type deficient in physical and mental energy."

Of the American mulatto one not infrequently meets with the assertion that he is on the average inferior mentally, morally and physically to either the white or the Negro race. Thus Doctor J. B. Taylor states ("The Negro and His Health Problem," *Medical Record*, September 12, 1912) that, "it is demonstrated by well-attested facts that these hybrids of black and white are vastly more susceptible to certain infections; their moral as well as physical stamina is lower than that of either original race." Others would deny that conclusive evidence to this effect exists. Professor Eugene Fisher, for example, regards favorably the Hottentot-Boer breeds of German Southwest Africa. Various mental tests agree in showing that in general the negro is inferior mentally to the whites and that the mulatto is intermediate. However, it is certain that under existing social conditions in our own country only the most worthless and vicious of the white race will tend in any considerable numbers to mate with the negro and the result can not but mean deterioration on the whole for either race. Superior stocks of any race have nothing to gain and much to lose by crossing with stocks of lower mental level. In human relations it is not alone a question of biological inheritance but likewise of social inheritance. The greatest unhappiness that is likely to arise out of race-crossing is through the disturbance of this social inheritance. The social environment under which such crossing occurs and in which the hybrid is compelled to live can not be ignored in any problem of racial miscegenation.

There is certainly not one iota of evidence that the crossing of any two widely different human races will yield superior offspring in any respect. Our evidence derived from plant and animal breeding except under conditions of experimental control is in general against pronounced crosses. The inferiority of the mongrel, in spite of possible hybrid vigor in the first generation, is universally recognized. No sensible farmer, for example,

would seek to improve his Jerseys or his Herefords by crossing one with the other. It is true that in pure breeds of plant and animals we sometimes venture on a cross to introduce some new desirable character but we follow up such mixture by a rigid selection in which is eliminated all but the rare individuals having the desired characteristics, and we continue this elimination generation after generation to fix the characters again. It is obvious that no such selection as this would be possible among the progeny of human crosses.

It clearly becomes our duty then to determine as accurately as possible the degree of non-relationship between races it is inadvisable to transcend in interracial marriages. Where parent racial types differ in a considerable number of hereditary factors, while characters appear to blend and become more or less intermediate in the first generation hybrids, such little scientific study as has been made on the second generation of human hybrids gives indications of a high degree of variability and a random assortment of more or less inharmonious traits. This is what would be expected on the Mendelian basis. One can not look at the many faces photographed in Fischer's book on the Rehoboth hybrids of South Africa, for example, without being impressed by the diverse combinations of ancestral features exhibited. It is probable that where there is a pronounced alternative inheritance of many traits various unfortunate combinations are likely to result from time to time. We are certainly taking great risks in accepting in any considerable numbers into our country those races we can not assimilate to advantage.

CHAPTER XXIII

RACE BETTERMENT THROUGH HEREDITY

Most of us have heard in one form or another the story of the youth on adventure bent, who was captured by the giant and under dire penalty in case of failure was set the task of sweeping out the giant's stable before sundown. The peculiarity of this stable, it will be recalled, was that, as fast as the refuse was swept out at the door an even greater quantity poured in through the windows so that the sweeper, just in proportion to his zeal, became more and more encumbered with his burden.

Questionable Charity.—Though we smile at the childishness of this legend, are we not as a civilized people attempting through our charities a feat parallel to that of this unfortunate youth? We foster and favor our social wastage with the inevitable result that it runs riot under our sheltering hand and deluges us with an ever accumulating flood of its like. For are we not constantly building more asylums, sanitarium and prisons, to preserve more unfit, to produce more defectives, to require still greater numbers of asylums, sanitarium and prisons, to preserve more unfit, and so on in unending progression?

Past Protests.—At nearly every period of history there have been certain individuals who have seen the necessity of a state eliminating its supply of defectives. For instance, we find the importance of this strongly urged by Plato. After pointing out the fact that the shepherd, in order to maintain the standard of his flocks, bred only from the best individuals, as did likewise the huntsman with his dogs and horses, and the fancier with his various pets, Plato went on to show the danger to the state of allowing the constantly increasing body of defectives and degenerates to multiply their kind. Repeated expression of the same idea has occurred from time to time during the succeeding centuries.

Little heed was paid to these remonstrances, however, with the result that is known to us all. To-day, "the glory that was Greece and the grandeur that was Rome" is still sung by the poet, but the original nations themselves have long since passed into the night.

An Increasing Flood of Defectives.—Strive to ignore the the unpleasant facts as we may, we have to admit that the same problem of what the human harvest shall be is with us in grave form to-day. The alarming phase of the situation, however, lies in the fact that we seem to be facing an ever increasing flood of social wastage.

But *why* this increase of defectives? It can not be attributed to oppression, to grinding poverty, or to decline in attention to our sick and needy, for never was prosperity greater, never were charities more flourishing, never such activity in the search for palliatives and cures. The simple fact is that we are breeding our defectives. The human harvest like the grain harvest is based fundamentally on heritage. And to get a better crop of human beings, we must, as with other crops, weed out bad strains.

To whatever source of information we turn the facts are essentially the same. Abroad we find that in England, for example, the ratio of defectives to normal more than doubled between 1764 and 1896. At home, from the investigation of Davenport and Weeks we learn that in the state of New Jersey the number of epileptics doubles every thirty years. And other investigators estimate that the fecundity of mental defectives in general is about twice as great as that of the average of our population. In a former report of the New York State Board of Charities we read, "There are about thirty thousand feeble-minded persons in the state of New York, of whom four thousand are intermittently sequestered while twenty-six thousand who are a menace to society are at liberty and may produce the unfit." And a passage from a Massachusetts report reads as follows: "We have been obliged to refuse a very large number of applicants for the admission of feeble-minded women—many of whom have given birth to one or more children. The prolific progeny of these women almost without exception are public charges from the date of their birth."

How fertile defective types may be is shown by a passage in one of Doctor Wilmarth's papers which runs as follows: "One feeble-minded woman, now removed from this state, had by different men eighteen children in nineteen years, she alleges." In a letter Doctor Wilmarth told me that the birth of the twenty-third child of this woman had just been announced! In one English workhouse Potts reported sixteen feeble-minded women

who have produced one hundred sixteen mentally defective children, and Branthwaite ninety-two female habitual drunkards who have had eight hundred fifty babies. If we include two million individuals cared for annually in various institutional homes, hospitals and dispensaries as dependents, the estimated total of insane, feeble-minded, epileptic, deaf and dumb, criminals, juvenile delinquents, paupers and other dependents in the United States in 1910 was approximately three million, or one in every thirty of our population! With the higher fertility of certain of these classes and with only a small percentage under custodial care where will it all end?

Natural Elimination of Defectives Interfered with.—With our improved methods of sanitation and care of the sick, the pauper and the defective, these classes have been freed in part from the stress of an environment that under natural conditions would have resulted in their premature death and consequent infertility. In fact, we have, temporarily at least, so eased the rigors of what the biologist calls *natural selection* that decadent stocks are not only holding their own, but some of them are increasing relatively faster than normal stocks. Moreover, they are contaminating sound strains. It is clear, therefore, that if we do not use our intelligence and substitute some other check, we are headed toward disaster.

Human Conservation.—We talk much in recent years of *conservation*; but what are our forests and frontiers, our minerals and our waterways, compared with our national health and life-blood? No farmer would think of setting aside a diseased or physically defective *animal* for breeding purposes, yet the same man together with the majority of mankind is wholly oblivious to similar faults when it comes to the mating of human beings. But is it not as important to look to fitness in man as in Poland China hogs or Holstein cows? Certainly the various strains are as marked and breed as true in the human family as in our live stock. Why face complacently in our own families what we would not tolerate in our piggery?

From the expenditure of comparatively small sums in studying the inheritance of various qualities in wheat, corn and other grain, improvements based on the laws of genetics have been secured which are enormously increasing our agricultural output and thereby adding to our national wealth. But if it costs relatively little to discover and conserve millions of dollars' worth

of hereditary qualities in our plants and animals, what are we to think of ourselves, an intelligent people who, knowing that "every good tree bringeth forth good fruit, but a corrupt tree bringeth forth evil fruit," still go on placidly permitting the production of defectives and delinquents? We are all familiar with the fate of Babylon, Assyria, Persia, Egypt and Rome. Why not America? Certainly we have no pledge of special immunity from Divine Powers.

Why Not Prevent Our Social Maladies?—There is no reasonable person, I think, who will not admit that the motives underlying our modern altruistic practises are the noblest fruitage of our slow upward struggle from the brute to man. As humane beings, we can not cast aside these principles and return to the painful and pitiless method of nature which would leave the sick and the defective alone to perish miserably; the sacrifice would be too great.

Is there then no escape from this dilemma? To this query the modern students of heredity answer yes; let us but add more wisdom to our charity and the enigma is solved. We need no sacrifice of pity but rather an expansion of it. Let us but extend our vision from immediate suffering to the prospective suffering of the countless unborn descendants of our present unfit and ask ourselves the question, why should they be born? Havelock Ellis well says, "The superficially sympathetic man flings a coin to the beggar; the more deeply sympathetic man builds an almshouse for him so that he need no longer beg; but perhaps the most sympathetic of all is the man who arranges that the beggar shall not be born." Why not prevent our social maladies instead of waiting to cure them? This is the province of eugenics.

Eugenics Defined.—The term Eugenics was coined in 1883 by Francis Galton in his book entitled *Inquiries into Human Faculties*, and we may therefore look to him for a satisfactory definition. He says, "Eugenics is the study of the agencies under social control, that may improve or impair the racial qualities of future generations, either physically or mentally." And again, "I take Eugenics very seriously, feeling that its principles ought to become one of the dominant motives in a civilized nation, much as if they were one of its religious tenets. . . . Man is gifted with pity and other kindly feelings, but he also has the power of preventing many kinds of suffering. I conceive it to fall well within his province to replace natural selection by other

processes that are more merciful and not less effective. This is precisely the aim of Eugenics. Its first object is to check the birth-rate of the unfit instead of allowing them to come into being, though doomed in large numbers to perish prematurely. The second object is the improvement of the race by furthering the productivity of the fit, by early marriages and the healthful rearing of their children."

Improved Environment Alone Will Not Cure Racial Degeneracy.—While many an enthusiastic humanitarian is laboring under the assumption that if we can improve external conditions human deficiencies will disappear, the student of heredity realizes that this is in large part a delusion unless we can secure an accompanying improvement in intrinsic qualities of the human species itself through the suitable mating of individuals. Just as the intelligent farmer to-day demands selected seed as well as good soil and proper cultivation, so one with the facts of heredity at hand would, as he views social problems, urge the fundamental importance of having selected stock with which to start. No shifts or shapings of environment will ever enable men to "gather grapes of thorns or figs of thistles."

The Problem Has Two Phases.—The thoughtful student of human heredity sees the dangers confronting us and is advocating two distinct programs: he would (1) encourage the reproduction of the best, and (2) prevent the mating of the unfit. Through the first he hopes to augment the numbers of our superior strains. Through the second he hopes to avoid further contamination of normal stocks and to bring about the gradual reduction of defective ones. It is evident that these are two essentially distinct problems although the practise of either method would result in racial improvement. The first is sometimes spoken of as *positive* or *constructive eugenics*, the second as *negative* or *restrictive eugenics*.

National Menaces.—While many factors may tend toward national deterioration, the four most prominent ones which are operative in, or which threaten a nation are: (1) war; (2) the unwise charity which not only permits but encourages the production of unfit strains; (3) the immigration of types which in desirable natural attributes do not measure up to national standards; and (4) the infertility of better stocks.

War.—It is clear that any race must be carried on by what is left after war has taken its toll. And just in proportion as

it takes a toll of men of above average in physical efficiency, energy and intelligence, just in that proportion are future generations impaired. How serious such reversed selective action is, is determined by the deadliness of the warfare and the length of time it continues. Presumably when armies are assembled from volunteers, instead of by conscription, there is the greatest danger from the eugenic standpoint, since not only physical but ethical qualities are involved. While it is very difficult to appraise the motives which lead men to enlist for war, in so far as volunteers are men of greater bravery, loyalty and high sense of duty than are conscripts, the volunteer system is deplorable.

An argument that has been advanced for the beneficial effects of war is that a stronger or superior race comes to replace an inferior one. This is certainly not true of modern warfare between civilized nations. Again it has been claimed that not only the less resistant individuals are weeded out of the ranks by disease and the rigors of military camp-life but the hardships of war are also reflected on to the non-combatants so that the weaker members of the civilian population are eliminated, leaving a higher average quality of survivors. To whatever extent this is true it is probably very far from offsetting the eugenic drain entailed by the loss of first-class fighting men.

The Penalty of Unwise Charity.—It is obvious that on a mountain highway we can build a strong railing at the top of a precipice to prevent accidents, or we can establish ambulance and hospital service at its foot so that unfortunates who plunge over may be tenderly cared for or decently laid out by the undertaker. It is all a matter of judgment. At present in our charitable work we are using mainly the hospital and undertaker combination. Lest it be thought that the alarm over the possible deterioration of our blood as a nation is based on rhetoric rather than on reason, the reader is requested to re-read the chapters on mental and neural disorders (Chapt. XIX) and crime and delinquency (Chapt. XX). If, as the available evidence appears to show, decadent stocks are increasing excessively in comparison with better strains, then the only intelligent thing for society to do is to keep the race purged of the physically and mentally incompetent by instituting an intelligent social selection which will accomplish humanely the same beneficent result that natural selection would secure mercilessly. This vicious or defective horde could in a single generation be materially lessened by preventing parenthood of the plainly unfit.

Immigration.—The dangers to a country which may lie in the immigration of inferior strains has already been discussed at some length in Chapter XXII, and the subject is only introduced at this point again to recall the facts in their proper eugenic setting. The problem is a particularly serious one for the United States which already has a large undigested and possibly indigestible foreign population, and into which further hordes of immigrants are hoping to enter. It is clearly the duty of our nation to refuse to have foisted upon it an incubus of degeneracy and incompetency for which it is in no way responsible.

Infertility of Better Stocks.—We look grave at the suggestion of what may happen as the result of the destruction of half a million able-bodied men in war, and well we may, yet we face with complacency what is happening to our race through the celibacy, the delayed marriages, and the infertility after marriage of thousands of our mentally and spiritually most highly endowed men and women. Yet from the standpoint of racial preservation, what is the difference how parenthood is prevented, so long as such frustration is a fact?

Are not the able-bodied and able-minded men and women who refuse to marry and rear children fit to carry on civilization as much shirkers in their duty to their nation as the coward who slinks away from the dangers of war? Why in all fairness should we not broaden the term "slacker" to include the race-slacker? If it is necessary for the defense of our race to send the flower of our manhood to death on the battle-field, what about the flower of our womanhood? What about the capable men who remain unmarried? Why go out and fight for a race that will soon not exist? Surely it is just as important to give lives *to* a nation as to give lives *for* it. Is there anything of greater importance in the world than the breeding and rearing of the right kind of citizens? If the increased leisure which comes to the successful nation means merely relaxation and amusement with consequent loss of the sense of responsibility, if it means leaving the nation to the procreative recklessness of the illiterate foreigner or the mentally subnormal, then, indeed, is the prospect a gloomy one.

The need for individuals of superior physical, mental and moral qualities to multiply is so obvious as scarcely to require comment. Yet the fact is that judging from all appearances these

are the very ones who have the lowest birth-rate. Eugenics is mainly concerned with the relative rates of increase of the various classes, not with mere fertility in itself. And the actual increase must be measured in terms of the extent to which birth-rate exceeds death-rate. If a high birth-rate is accompanied by a high death-rate then it is not especially significant in increasing a given class as a whole. All available evidence points to the fact that to-day the lower strata of society are far outbreeding the middle and higher, with an almost negligible difference in death-rate, and just in the measure that these lower strata are innately inferior just in that degree must the race deteriorate. The seriousness of the whole situation as it exists to-day hinges, therefore, on the extent to which the lower strata are inferior to those above them.

An Unselected Population May Contain Much Valuable Material.—In evaluating these lower strata a matter of very great importance is whether the population is a selected or an unselected one. If the population has been long resident in a given region and has had fairly good opportunity for education then we will find in the lower reaches a larger percentage of sedimentation made up of the worthless and inferior stocks. If, however, a continual fomentation and geographical shifting of the population is in progress as in parts of America, or if adequate educational opportunities are lacking, as in some parts of Russia, the poor and less well-to-do classes may contain, no one can tell how much, relatively valuable stock.

Forel remarks on this point as follows:

“If we compare the nature of delinquents, abandoned children, vagabonds, etc., in a country where little or nothing has been done for the people (Russia, Galicia, Vienna, etc.), with that of the same individuals in Switzerland, for example, where much has already been done for the poor, we find this result: In Switzerland, these individuals are nearly all tainted with alcoholism, or pathological heredity; they consist of alcoholics, incorrigibles, and congenital decadents, and education can do little for them because nearly all those who have a better hereditary foundation have been able to earn their living by honest work. In Russia, Galicia, and even in Vienna, we are, on the contrary, astonished to see how many honest natures there are among the disinherited when they are provided with work and education.”

The Lack of Criteria for Judging Fitness.—Barring the untold hordes of actual defectives who have gravitated into this lower stratum, there are few positive criteria by which we can measure the real fitness of the remainder. Before we can set out on a campaign of positive eugenics we must have some standard by which to steer, and it would be a rash advocate indeed who would assert that class distinction alone, or even success as measured by public opinion to-day should be our whole criterion of fitness. Shall we measure fitness in terms of how successfully one can acquire worldly goods, or in other words, by the property test, or what shall be our standard?

Native Ability, Independence and Energy Eugenically Desirable.—Although we can not sift out with certainty the superior from the inferior in our normal population by the property test or the educational standard alone, it is undoubtedly true that, on the whole, native ability, independence and energy are present to a higher degree in our well-to-do and prosperous families than in the stocks which merely hold their own or which gradually decline, and there is no gainsaying the fact that in so far as the lower classes are where they are through actual deficiency—and there are enormous numbers in this category—they threaten our very existence as a race. It is imperative that the great middle-class in particular establish in some way a selective birth-rate, by increased fertility on their own part, and diminished fecundity on the part of inferior stocks, which will offset or more than offset the disproportionate increase of the socially unfit.

Four Children to Each Marriage Desirable.—It is estimated that under present conditions an average of about four children should be born to each marriage if a stock is to maintain its numbers undiminished. Some of our most valuable strains are falling far short of this average. In a statistical table on the relative fertility of different stocks, prepared by Pearson, we find the mentally defective, criminal, deaf-mute and degenerate stocks heading the list with averages ranging from five to seven children per family, while the American graduate (based on Harvard statistics) and the English intellectual types average less than two children per marriage. While the death-rate is higher in the undesirable classes mentioned, it is by no means enough higher to compensate for the difference in birth-rates. Thus while certain very desirable types are not maintaining them-

selves genetically, other extremely undesirable ones are rapidly more than replacing themselves. Investigations made by Heron in London show that this condition as regards English desirables did not exist sixty years ago; then the richer a community was in professional men and well-to-do families, the higher was the birth-rate. Rowntree has found that the age of skilled workmen at marriage is distinctly higher than that of unskilled workmen.

In Massachusetts, where for many decades birth statistics have been taken on a basis of nativity, the records show that the birth-rate of the native group is only fourteen per thousand, while the death-rate is eighteen per thousand. The native American stock in general, in fact, appears not to be holding its own. According to the twenty-eighth report of The Immigration Commission, 13.1 per cent. of American women under forty-five years of age who had been married ten to nineteen years, were childless; and of those who had children, the average was only 2.7 children per woman.

Sprague, from a study of vital statistics, calculates that for the American stock of the East, at least, every mother must average 3.7 children for the stock barely to maintain itself. The American women just mentioned, therefore, were falling far short of the percentage required. Speaking of the celebration of the three hundredth anniversary of the landing of the Pilgrims, Holmes, from a study of this stock in California, graphically points out (*Journal of Heredity*, November, 1918) that if its present birth-rate continues for another 300 years, it will be possible to put all the surviving descendants back into the *Mayflower* without overcrowding.

From a study based on the results of questionnaires sent to native-born American families throughout the Middle West which included some 750 families of a generation ago and 2,500 families of their descendants in this generation, Ross and Baber, in 1924, concluded that "among Americans of native parentage belonging to the middle-class in the Central United States, the shrinkage in family size between the present generation whose families are filled, and their parents is $38\frac{1}{2}$ per cent." The present generation of these families averages 2.8 children to a couple, with 13 per cent. of the unions childless and nearly 18 per cent. with one child. In an independent study published in the same monograph (*No. 10, University of Wisconsin Studies*)

Miss Halverson found that 100 dependent families investigated reared an average of $6\frac{1}{2}$ children per family.

Factors Contributing to Low Birth-Rate in Desirable Strains.—Most students of the subject believe that the fecundity of much of the best blood in our country has reached such a low ebb as to threaten the whole fabric of our commonwealth. How to correct this is the pressing problem to which no one has found a solution. However much one may deplore it the fact remains that always in the history of the civilized world with the rise of material conditions in any class of a population there has come an accompanying limitation of childbirth. Explain this as we may in modern times—whether as an awakened individualism which looks only to the immediate interest of the individual as against the ultimate interest of the race, or a desire for luxuries or for a better opportunity for smaller numbers of children, or as a determined effort of the wage earner to better his conditions, or to the feminist movement with its accompaniment of a greater personal freedom of married women and the recognition of the fact that marriage and child-bearing are often bars to employment, or to general increasing pressure of economic burdens—in brief whatever the cause or causes, there is no denying the fact of a diminishing birth-rate among our abler men and women. Moreover, no amount of coaxing, cajoling or dire prophecy seems to avail in altering the conditions. Various partial remedies, many of them of questionable practicability, have been proposed, but so far there has been no far-reaching effort made to put any of them into effect. It has been suggested that society return to the simple life so that our young folk may marry earlier and live more easily on limited means, but so far few volunteers have appeared to lead the procession. While there is no doubt that present economic conditions tend to penalize parenthood, the simple life will not return for the mere asking. It has been pointed out that the father is in unfair competition with the bachelor and is also unfairly taxed in comparison, and some would therefore tax unmarried men more heavily. Others would pay a direct bounty on reproduction, but it is probable that such rewards would merely stimulate families of the lower types to increased fruitfulness. And so one panacea after another may be weighed and found wanting.

The College Graduate.—Many of our modern critiques of the birth-rate situation make much of the fact that our college

graduates as a group are scarcely reproducing themselves. According to Davenport, Bryn Mawr College between 1888 and 1913 has graduated 1,193 bachelors of arts, but these women have produced up to January, 1913, only 263 girls to take their place in the next generation. He also points out that statistics on some of the graduate classes of Harvard of twenty years ago or earlier show that they are little more than maintaining themselves; thus one class of 328 graduates twenty years later had produced 195 sons, and in another case a class of 278 individuals had produced, twenty-five years later, 141 sons. Relatively similar statistics can be cited for other eastern colleges.

According to records of college classes far enough back to insure complete histories only a little more than 50 per cent. of the graduates of women's colleges, and only about 75 per cent. of the graduates of men's colleges in the United States marry. Graduates of coeducational institutions have a higher marriage-rate to the extent of from 5 to 9 per cent. Data from classes graduating from various women's colleges before 1901 show that they were on the average producing less than two children per family to replace themselves and their husbands. While the graduates of men's colleges had a somewhat greater birth-rate during the same period they were still falling short of three children per family. From an investigation of families of American men of science, in which the age of the parents show that the family is complete, Cattell finds the marriage-rate high (895 of the thousand studied) but the birth-rate very low. Among 261 completed families he found an average of 1.88 children per family, about 12 per cent. of whom died before maturity. In other words Cattell finds that the scientific man has about seven-tenths of an adult son.

All such cases of college graduates cited as effecting especially deplorable declines in birth-rate are based on the assumption that these individuals are a particularly superior stock.* One might question this premise as a generalization. It may or may not be true. Are they superior or have they had mainly a combination of luck and incentive, luck in that their parents had sufficient means, acquired possibly through their own supe-

* For arguments indicating the superior eugenical fitness of college graduates see "Wellesley's Birth-Rate," by Roswell H. Johnson and Bertha Stutzman, *The Journal of Heredity*, June, 1915. See also, "Education and Race Suicide," by Robert J. Sprague, *ibid.*, April, 1915.

riority, possibly not, to send them to college, and incentive derived from a fortunate environment which awakened a desire in them—or in their parents for them—for college education? Is the woolly-witted son of wealth so abundant in our colleges to-day, who is boosted through by hook or by crook, of superior eugenical value to the alert eager boy—and his name is legion—destined for economic reasons to go to work at or before the completion of his high-school course, perhaps because of the very fact of an unlimited fecundity in his own family which necessitates his help for the general support?

When one first learns of the declining birth-rate among college women and men he feels appalled, but immediately the question flashes up, if this is *the* superior stock, and up to date it has died out or is dying out rapidly, whence then this ever augmenting rush of young folk who fairly deluge our universities and colleges to-day? Does it not rather point to the fact that in our own country at least, the man who will and can take a college education successfully is not so much the product of breeding from college men, as of a prosperity which leaves a sufficient surplus in the family exchequer to enable sons and daughters to go to college, and is it not reasonable to suppose that there is yet an abundant stock back of these who similarly await but the golden touch of opportunity? When we consider such men as Carlyle, Lincoln and a host of others who were not the sons of collegians, although we may be university pedigreed ourselves we can not but feel doubtful of the validity of a premise which takes a college stock unqualifiedly as having any considerable monopoly of innate superiority. After all, college can mean little more than opportunity, and the obtaining of such opportunity in this world of economic maladjustments and accidents of social position is too largely a matter of chance, at least in America, to stamp the possessors of these advantages, on this criterion alone, as of inborn superiority. Undoubtedly much that is intrinsically good now slumbers in the lower strata of society because of lack of favorable environment to call forth the latent possibilities.

Constructive Eugenics Must Be Based on Education.—As to the first phase, direct selection for superiority, the campaign must, in the very nature of things, be one of education. With the necessary knowledge of the facts in mind, the awakening conscience of the individual together with an enlightened public

opinion will form the safest guide. Increasing popular comprehension of the inevitable nature of human inheritance must engender a sense of responsibility as to the positive eugenic fitness of a contemplated marriage. The growth of this sentiment will doubtless be slow, and properly so, for as yet we have but half-lights on what are the most desirable types of humanity. No one can say what the highest type of man should be, but almost any one can readily pick out types which certainly should *not* be. The necessity of the situation must be driven home so that it becomes part and parcel of the collective intelligence of the educated public. Different ideals of life will have to be established in the young. If knowledge of the facts of heredity is thoroughly disseminated among the people and ideals regarding parenthood are fostered, then much will have been accomplished by the psychic power of suggestion alone toward the end desired.

Utilization of Family Pride as a Basis for Constructive Eugenics.—There are few more powerful incentives to make the best of one's abilities, or few greater deterrents from vice than family pride; and there is no reason why this same sentiment may not be aroused in behalf of unborn generations. The sentiment of caste or aristocracy in some form is well-nigh universal in mankind. The family of Mr. A came over in the *Mayflower* and is therefore worlds above the family of Mr. B, who arrived fifty years later. Mr. X's income is \$5,000 a year, Mr. Y's only \$1,500. The poor family in the front suite of the tenement regards itself as far superior to the one in the rear. Among criminals the professional house-breaker feels himself to be of higher caste than the sneak-thief, and in turn is surpassed by the bank burglar. Even in the insane asylum the feeling is rampant. With such a wide-spread tendency for a foundation the creation of a sentiment of eugenic aristocracy is by no means a visionary undertaking.

The Tendency for Like to Marry Like.—Even now there is a decided though unconscious tendency for like to marry like and thus create particular strains. We have lines, for instance, which produce notably families of scholars, others which yield mainly statesmen, and still other strains of inventors, of financiers, of naval men, of soldiers, and of actors respectively. And there is little doubt that people, with the facts of inheritance of ability once before them, will be led to act more or less in accordance with their knowledge. On the other hand, due appar-

ently to the same unconscious tendency for like to marry like, we find produced criminalistic, feeble-minded, deaf-mute and tubercular stocks. The first type of family is often termed *aristogenic* and the second or defective type, *cacogenic*, or *dysgenic*.

Public Opinion as an Incentive to Action.—Much of our social conduct is the result of the pressure of public opinion, yet so accustomed are we to this that we ordinarily do not feel it as a hardship. There is little doubt that similarly the more wholesome attitude toward parenthood advocated by the eugenist would be taken as a matter of course, once the idea became prevalent. It would come to be one of those socially preconceived ideas which are as much actualities and which become unconscious guides to action no less certainly than do the more obvious personal habits of the individual. And just in the degree that we as a race get the “feeling” that intellect, morals and skill are highly desirable attributes in marriage selection, just in that degree will one’s affections in their earlier stages gravitate toward individuals who possess such qualities in high degree. In the main, those stocks which have shown by ancestral as well as personal achievement their superiority will tend to insure most certainly a continuation of this superiority in offspring.

Choosing a Marriage Mate Means Choosing a Parent.—Although marriages, as all young folk know, are made in Heaven, it is interesting to see what a vast number of these foreordained matches coincide with propinquity in college, in church, or in the same social set. Moreover, children are born here on earth. The one thing of all things that the eugenist desires is for these young folk to get a clear-eyed vision of the fact that in choosing a marriage mate they are also choosing the future father or mother of their children with all that this implies.

The Best Eugenic Marriage Also a Love Match.—A few recent writers, who show an utter misconception of what the aim of modern eugenics is, have raised the cry of give us the old-fashioned love match instead of the eugenic marriage, as if the eugenist’s ideal of moral cleanliness, freedom from transmissible physical taints or mental enfeeblement, and an attitude of special approval toward marriages which bring together individuals of more than average mental or spiritual endowment, had anything in it that was inimical to love. No one better

than he realizes the sordid depths to which marital relations devoid of mutual affection and regard must reach. Certainly there is nothing in the eugenic ideal when its full import is understood that can shock the sensibilities of the most delicate-minded. Indeed it is people of fine susceptibilities who will be the first to feel repugnance toward a marriage which means mental or physical deterioration of their own blood.

Good Traits No Less Than Bad Ones Inherited.—An inspection of such charts as those shown in Figs. 100, 101 and 102, pp. 427, 428, 430 and an abundance of such encouraging records may now be found—reassures us in our convictions that good traits are no less inheritable than bad ones. And what any healthy, mentally well-endowed person may be depriving the world of if he or she declines to enter into a fruitful marriage

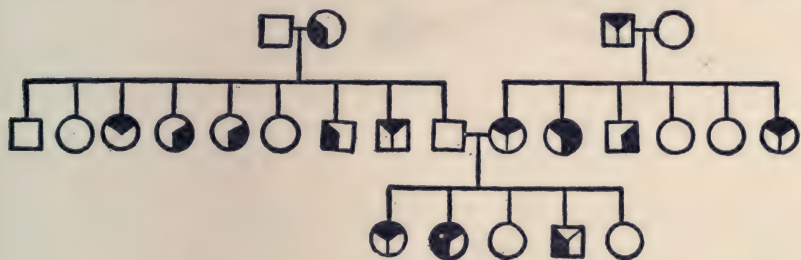


FIG. 100

Pedigree of family with artistic (dark upper section), literary (dark right section) and musical (dark left section) ability (from Davenport).

can not be better exemplified than in the following excerpt from Davenport:

“Many a man at the opening of his life work vows, as Judge John Lowell of the middle of the eighteenth century did, as he was being graduated from Harvard College, that he will never marry. But nature was too strong for John Lowell and he married three times and among his descendants was the director of a great astronomical observatory, the president of Harvard College, a principal founder and promoter of the Massachusetts General Hospital and the Boston Atheneum; the founder of the city of Lowell and its cotton mills; the founder of the Lowell Institute at Boston; the beloved General Charles Russell Lowell and his brother, James, both of whom fell in the Civil War, and James Russell Lowell, poet, professor and ambassador;

besides brilliant lawyers and men entrusted with large interests as executors of estates. Do you think John Lowell would have taken that vow could he have foreseen the future?"

The Elimination of the Grossly Unfit Urgent.—But even if, under present conditions of partial knowledge and lack of an adequate standard, the constructive phase of eugenics must be left in the main to the awakening conscience of the individual as humanity improves in general enlightenment, the second phase, the elimination of the grossly unfit is one of the greatest social obligations that confronts us to-day. For if there is an alarming amount of mental impairment in civilized nations, and if the problems of pauperism, inebriety, prostitution and criminality

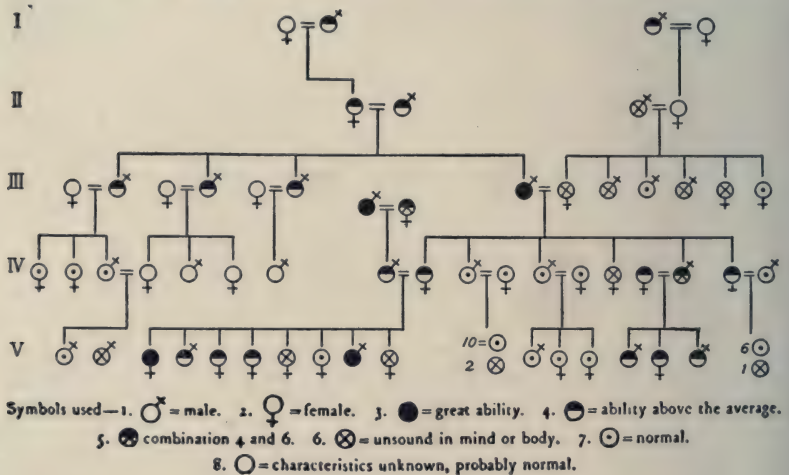


FIG. 101

Inheritance of ability (from Kellicott after Whetham).

are closely interwoven with the problems of mental unsoundness, as we have every reason to believe from available data, then any means which will operate toward securing normally functioning brains will at the same time operate toward diminishing defects and delinquencies. And inasmuch as a considerable proportion of defects, both mental and physical, are inheritable, it is obvious that if we can diminish the number of children born into the world with defective brains or bodies we have made a long stride in the right direction.

Suggested Remedies.—But how go about it? Various schemes have been proposed, of which the chief are as follows:

1. Laws restricting marriage.
2. Systems of mating with the purpose of covering up and gradually diluting out defective traits.
3. Segregation during the reproductive period.
4. Sterilization.
5. Education in the principles of eugenics.

Inefficacy of Laws Which Forbid Marriage of Mental Defectives.—The utter inefficacy of the first proposition, namely the enactment of laws restricting marriage, at least as regards the socially unfit whose condition is based on impaired mentality, has been demonstrated time and again. If they are forbidden marriage, they merely have children without getting married. Most states have laws to prevent the marriage of such individuals but these laws are almost wholly ineffective in preventing procreation on their part. We might as well recognize once for all that in such cases nothing short of close custodial care or sterilization will accomplish the end desired.

As to the second proposition, systems of mating with the purpose of covering up and gradually diluting out defective traits, this has been shown to be possible with certain types of defectives. Whether it is desirable or not is a different question.

Systems of Mating Impracticable in the Main.—By systems of mating, it should be said, is not meant the arbitrary marrying of two individuals willy-nilly, but rather it is the prevention of marriage of two individuals having similar defects. In general the facts at our command indicate that in the majority of cases the offspring from a marriage of an insane, feeble-minded or epileptic person with a normal individual free from all neuro-pathic taints are normal or at most show but slight effects of the taint. But what normal individual would knowingly marry into such a stock? With few exceptions such traits where inheritable are apparently negative, that is, not represented by some positive abnormal factor but due to the lack of some element or elements necessary to the proper working of the normal brain. In the offspring of such a union the necessary missing factors are supplied by the normal parent. Or in Mendelian phraseology, the defective traits are recessive and are dominated by the normality of the other parent. Such offspring, however,

while apparently normal of body are not normal of germ-plasm inasmuch as half of their germ-cells will carry the abnormality of the defective parent as earlier explained (page 201) under Mendelism. We have already seen (page 214) how by continually marrying into strong strains the liability to recessive defect can be diluted out until the descendants are no more likely to have defective children than are members of our ordinary population. If, however, as is estimated in Bulletin No. 5 of the Eugenics Record Office, about thirty per cent. of our general population already carry recessive neuropathic taints, it certainly is a hazardous proceeding to attempt thus to breed out nervous defects unless one is absolutely sure of the normality of the strain into which it is proposed to marry. The great

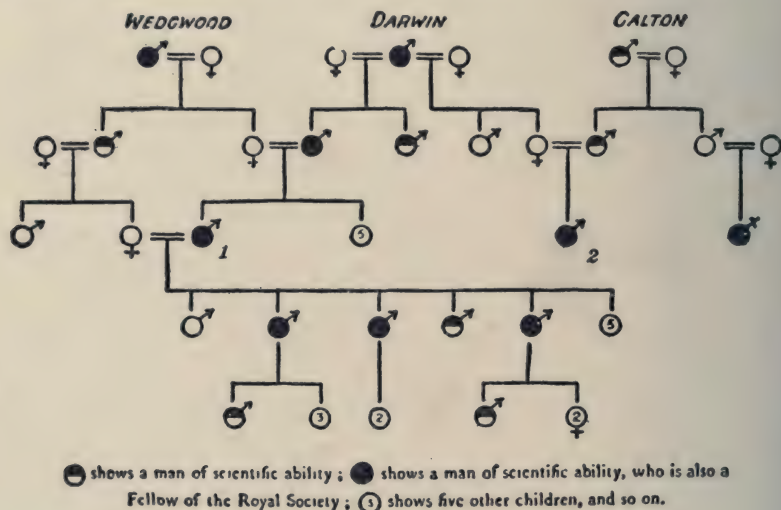


FIG. 102

Inheritance of ability (chart condensed and incomplete) in three markedly able families (from Kellicott after Whetham) :

1, Charles Darwin; 2, his cousin, Francis Galton, founder of the modern eugenic movement.

difficulty is in determining whether or not there is a defective ancestry in a given stock. We have at present no criteria for identifying normal individuals who have defective germ-plasm. As a practical test, however, if no defect has appeared in the stock for three or four generations back, the marriage would

be relatively as safe as are the marriages of our average population to-day.

Corrective Mating Presupposes Knowledge of Eugenics.—But such a scheme of corrective mating presupposes a relatively high degree of intelligence and judgment on the part of the participants, and this is just what we do not have and in the nature of things can not get, in the types of feeble-minded, epileptic and degenerate strains we are striving to eliminate. All our evidence shows that when unrestricted there is a marked tendency for feeble-minded to mate with feeble-minded, degenerate with degenerate. About sixteen per cent. of the feeble-minded, in fact, come from consanguineous marriages. If we try to legislate them into specific types of marriage then we encounter the same futility pointed out under our discussion of restrictive legislation, they will produce offspring without the formality of marriage.

In certain cases of insanity and in other than neuropathic defects one can see how the system might be inaugurated with greater prospects of success, but even then a knowledge of the principles of eugenics would be necessary to the participants, or in other words we could only accomplish our end through our fifth proposition, education.

Segregation Has Many Advocates.—As to the third proposition, segregation during the reproductive period, this seems to have a larger number of advocates than any other coercive measure. While on theoretical grounds it is plausible enough, when we face the actual putting of the method into practise we are confronted by the fact that tremendous sums of money would be required to sequestrate and maintain colonies or industrial refuges.

When one realizes that no state now provides for more than a small minority of its defectives, and knowing also of the pressure that must be brought to bear on legislatures to secure sufficient funds to provide for these cases of extremest urgency, one can not be overly optimistic about the practicability of extensive sequestration.

E. R. Johnstone, the superintendent of a large training school for feeble-minded in New Jersey, points out that no state in the Union is providing for many more than one-tenth of her feeble-minded and epileptics. If his estimate is true, to place in institutions, treat and train all its feeble-minded and epileptics would even now almost swamp any state treasury. But what

will it be in the future if we permit this unrestricted nine-tenths to go on and multiply their kind?

Leaving out of account the enormous sums spent in private charities even now from one-fifth to one-seventh the total public expenditures of almost any one of our states is going to maintain its defectives, dependents and criminals. Suppose, however, that we could get them all into institutions, institutional care at present by no means also implies prevention of propagation. It is not an unusual history of feeble-minded women in our county poorhouses that they alternate between periods of housework in some family and periods of residence in the almshouse, the return to the latter being only too often to bear an additional child.

Not a few students of the problem, however, advocate a rigid segregation as the only reasonable preventive measure, no matter what the expense. They point out that the cost is mounting higher each year and that we are only increasing it ultimately by procrastination. They urge, moreover, that when counting the cost of the segregation of the feeble-minded we should bear in mind also that we are reducing the expenses of our other charity and penal institutions, since much of degeneracy, pauperism and petty criminality centers in mental enfeeblement. Some believe that colonies can be established which are in considerable measure self-supporting.

Sterilization.—Since there is some considerable popular misunderstanding on the subject, it should be made plain that by sterilization is not necessarily, nor in fact generally, meant asexualization, or the removal of the reproductive glands. On the contrary, in the male, sterilization is ordinarily accomplished by an operation known as *vasectomy*, in which a small piece of each sperm duct is removed. It is a comparatively simple minor operation which involves no special inconvenience or hardship on the subject beyond the deprivation of offspring. In women the corresponding operation—resection of the oviduct—is termed *salpingectomy*. Here, however, the operation is a more serious one as it usually involves opening the abdominal cavity and the accompanying hazard of infection, a danger sufficiently great that it is safe to say that the operation will be resorted to more rarely than vasectomy in man.

As a Eugenic Measure.—Sterilization as a eugenic measure has many advocates and perhaps more opponents; and among the latter, it must be said, are many competent and thoughtful

students of the subject who recognize existing conditions and deplore their continuance as much as any one. They maintain that while we may have to come to it as a last resort, we are yet too ignorant of the actual effects of the operation, or are too little informed on the inheritability of the specific traits we are trying to eradicate, to launch forth on so radical a program. We must not forget that when we put sterilization into effect we are going to have to deal with individual cases, not general averages.

To What Conditions Applicable.—And just here, it seems to me, is the crux of the situation. When confronted by the defective individual, in a practical case, just what criteria are we going to use to determine whether this particular individual should be sterilized or not? Nearly all of the twenty-three states which have sterilization laws specify insanity, feeble-mindedness, epilepsy and criminality.

In Insanity.—When it comes to insanity I strongly suspect that those who have the selection of the examining board will have difficulty in finding an alienist who is willing to take the responsibility of deciding just which insane individuals shall be operated on and which not. For among the insane there are so many kinds and degrees of mental unsoundness, and these are of such varying and as yet unknown eugenical significance, that a positive decision is frequently out of the question. Of the twenty or more recognized forms of insanity who knows with any considerable degree of certainty which are heritable, which not?

Certainly the one fact which stands out conspicuously when we face most concrete cases, is that at present we need exhaustive studies of the inheritability of specific mental infirmities that we may know which warrant sterilization.

Yet on the other hand one of the most disquieting facts that confronts us to-day is the large number of patients who are on parole from our hospitals for the insane, subject to recall. What shall we do with them? Shall we submit them to the tremendous hardship of still remaining under custodial care although to all intents and purposes sane, or shall we make their release contingent upon their submission to vasectomy or salpingectomy?

In Feeble-Mindedness.—When we come to institutions for the feeble-minded, however, there seems to be much more unanimity of opinion among physicians in charge of such institutions that sterilization would be an effective and satisfactory

disposition to make of many cases, if we are to release the patients in question from custody. Unquestionably in cases of imbecility it is easier than in insanities to pass conclusive judgment on the inheritability of the condition in a large class of cases. Practically all are agreed that either permanent custodial care through the reproductive period or sterilization should be enforced. Some maintain that such individuals should remain permanently in institutions anyway and that therefore to sterilize them is needless, while others urge that if sterilized many capable of making their own living could be freed and allowed to do so.

According to Goddard the feeble-minded woman is about three times as likely to find a mate as a feeble-minded man, hence it would seem to be of much greater importance to sterilize the woman than the man.

Again it might be urged with much justification, that even though sterilized, the feeble-minded individual because of lack of self-control will transgress sexually and will thus certainly become a menace to society in the spread of venereal diseases.

In Cases of Epilepsy.—As to epilepsy, I find a very decided difference of opinion among physicians. Some consider it, on account of its apparently strong inheritability, together with the shocking crimes perpetrated by epileptic criminal types, one of the most serious menaces, while others point out that we know nothing of the real cause of epilepsy, that there are all degrees and shades, that it is probably referable to different causes in different cases and that no one is able to say what the offspring of any given epileptic will be.

In Criminal Types.—Here again we face the difficulty of deciding any particular case. Let us suppose that twenty-five per cent. of criminals are mental defectives, how shall we sift them out from the seventy-five per cent. who are supposed to be eugenically normal? Doubtless in many of the twenty-five per cent. class, the indications of defective mentality are sufficiently evident to prevent mistakes, but a considerable number of uncertain status must also remain near the border-line.

Sterilization Laws.—Since 1907 when eugenical sterilization was first legalized in an American state, twenty-three states have passed sterilization laws. In all, up to July 1, 1925, 6,244 individuals have been sterilized under such laws. For an elaborate source book of the entire subject the reader is referred to *Eugenical Sterilization in the United States* prepared by H. H. Laughlin of the Eugenics Record Office and published in 1922

by the Psycopathic Laboratory of the Municipal Court of Chicago. In his *Eugenical Sterilization; Historical, Legal, and Statistical Review of Eugenical Sterilization in the United States*, published by The American Eugenics Society, Dr. Laughlin brings the record down to January 1, 1926, and provides a critical analysis of the facts and tendencies, together with what he regards as "a model state law."

Social Dangers in Vasectomy.—It has been urged against vasectomy that it will work untold harm because it relieves of the responsibility of a probable parentage. This argument does not appeal to one as very weighty as far as the imbecile or other degenerate is concerned, because one of the very traits characteristic of such individuals is lack of any sense of responsibility. By this same token, however, we have a very good argument for sequestration as against sterilization, for the degenerate, even though sterilized, will not be restrained sexually and will be likely to disseminate venereal diseases or commit rape. Furthermore, there will be the temptation to sterilize and liberate certain types that would otherwise have been kept permanently in custody.

Our Present Knowledge Insufficient.—When all is said and done, after we take into account the meagerness of our present knowledge on the subject, it is not to be wondered at that many thoughtful students of a conservative turn of mind, feel that any considerable practise of sterilization is premature. The problem has so many phases, and despite occasional bits of positive knowledge, we are yet in such a sea of ignorance regarding it, that in no field is the good Friar Laurence's admonition of "wisely and slow; they stumble that run fast," needed more at present than it is here.

There is little doubt that in theory the feeble-minded and similar defectives should be sent to institutions and kept there, but the important practical question is, can this be done? We can have no final answer until it is tried. While the initial expense would undoubtedly be great, if we could keep our defectives from propagation for a single generation we could very materially lessen their numbers and in succeeding generations the expenses of their care would rapidly diminish.

The one crying need that stands out most prominently in this whole field is that of careful investigation of individual cases and specific types of malady, together with an accurate census of conditions as a whole. Our knowledge of individual

malign heredities is too meager to carry us very far at present. When we have found after adequate investigation in just which specific types of defects heredity is an important factor—and we shall undoubtedly find it to be one in many cases—then we can proceed confidently with sterilization, if it will prove to be more practical and desirable than sequestration.

Certain married degenerate types would seem to be the ones most urgently demanding attention. Having already begotten several defective children and with nothing else in prospect but the production of the same kind, it is difficult to see from any standpoint why a vasectomy on the male would not be a merciful act. There are not a few such families where the father is periodically in the hands of the law and yet not in permanent restraint. Once in custody his release could be made contingent on vasectomy.

An Educated Public Sentiment the Most Valuable Eugenic Agent.—Coming now to the last proposition, education of the public in the principles of eugenics, this is the method calculated to be of more far-reaching service than any other, in the negative as well as in the positive phases of eugenics. Education is necessary before we can have effective restrictive measures for the mentally incompetent established and enforced, and it is also a prerequisite to intelligent procedure on the part of normal individuals in considering their own fitness for marriage.

Of greatest importance in preventing undesirable marriages, as far as people of normal intelligence is concerned, will be the sentiment of disapproval which will arise on the part of society itself when it becomes really convinced that certain marriages are inimical to social welfare. Public opinion is, in fact, one of the most potent influences in marital affairs, simply because refusal to abide by the dictates of the community means social ostracism.

That social disapproval of certain unions can become a very real factor in preventing such marriage is evinced on all sides by the numerous barriers to marriage already in existence based on race, religious sect or social status. Even in our much vaunted democracies one is looked down on who marries "beneath" his or her social set. This sentiment of taboo, so readily and often so senselessly cultivated in our present human society, will inevitably spring up in consequence of a wide-spread knowledge of the facts of human heredity. It is to such a

growth, to the establishment of a disapproval which is the product of its own sentiments rather than to legislative enactments, that society must look for the greatest furtherance of the eugenic program.

Necessary as legal restraint is in certain cases, it must obviously be restricted to only the most glaring defects. Moreover, legislation can not run far in advance of public opinion.

The Question of Personal Liberty.—It must be admitted that there is a reluctance on the part of many even thoughtful individuals to the application of methods which savor in any way of restraint. An objection not infrequently urged by such persons against the application of certain eugenic principles is that they demand an unwarranted curtailment of personal liberty.

To those who hoist the flag of personal liberty, it may fairly be asked, how much personal liberty does the syphilitic accord his doomed and suffering wife and children, or how much personal liberty is the portion of the offspring of feeble-minded parents? Or, what quota of personal liberty will accrue to the ill-fated descendants of the epileptic, the habitual drunkard or criminal, the gross moral pervert, the congenitally deaf and dumb, or to even the progeny which may result from the union of two well-established tubercular strains?

We do not hesitate to send the pick of our stalwart healthy manhood to war to be slaughtered by the thousands and tens of thousands when an affront is offered to an abstraction which we term our national honor, and, sublimely unconscious of the irony of it all, we throw ourselves into a well-nigh hysterical frenzy of protest when it is proposed to stop the breeding of defectives by infringing to a certain extent on their personal liberties.

Society has already found it necessary to suppress certain individuals and yet we hear little complaint about loss of personal liberty in such cases. But if it is necessary to restrain the man who would steal a purse or a horse, is it not still more urgent to restrain one who would poison the blood of a whole family or even of an entire stock for generations? Surely there can be but one answer; society owes it to itself as a matter of self-preservation to enforce the restraint of persons infected with certain types of disease and of individuals possessing highly undesirable inheritable traits, so that perpetuation of such defects is impossible.

Education of Women in Eugenics Needed.—One of the most crying needs of the present is the awakening and educating of women to the significance of the known facts. For they are perhaps the greatest sufferers, and once informed, as a mere matter of safety if for no other reason, they will see the necessity of demanding a clean bill of health on the part of their prospective mates. Furthermore in the last analysis woman is the decisive factor in race betterment, for it is she who says the final yea or nay which decides marriage and thus determines in large measure the qualities which will be possessed by her children. Above all, young women must come to realize that the fast or dissipated young man, no matter how interestingly or romantically he may be depicted by the writer of fiction, is in reality unsound physically, and is an actual and serious danger to his future wife and children.

Much Yet to be Done.—But plain as is our duty regarding the application of facts already known, when we consider that the student of heredity has made only a beginning, it is equally evident that he must be urged on in his quest for new facts, and the establishment of new principles. There is imperative need to carry on proper experiments with plants and animals, to collect necessary data regarding man, and for what is scarcely less important, the publication of the facts already acquired so that the public may be guided aright.

Just at present it is of the utmost importance to secure more trustworthy statistics in order that we may intelligently go about instituting suitable restrictive measures for undesirable human strains. We must know the exact number and kinds of feeble-minded, epileptic and insane in our population, and we must have more insight into the personal status and pedigrees of our delinquents and criminals. For purposes of rational procedure such information is indispensable. Much can be done by hospitals, "homes" and penal institutions by determining and recording more accurately all obtainable facts regarding the ancestry of their charges. Moreover, in such states as Wisconsin, where the state hospitals for the insane have each an "after-care-agent," the duties of such officers might well include the collection of adequate data regarding the hereditary aspects of their patient's condition. And lastly, if in every census, whether state or national, it were made an important part of the work to secure accurate vital statistics, particularly as they pertain to human

heredity, the contribution toward enabling us ultimately to purge the blood of our nation of certain forms of suffering, degeneracy and crime would be inestimably great.

A Working Program.—And now after reviewing at some length various aspects of man's hereditary and congenital endowment, the important question arises as to whether it is possible, with the knowledge at present available, to go ahead with a practical program which will insure to the child of the future its right of rights, that of *being well-born*. When one considers the matter it is evident that much can be done at once. Most of the needs set forth in the preceding paragraph can clearly be met in a fair degree by instituting the procedures indicated.

One of the obvious duties in a restrictive way that confronts us right at the start is the care and control of the feeble-minded and of the defective delinquent in such a way as to prevent procreation. Much help can be given also through intelligent agitation for the establishment of colonies for epileptics and the higher grades of feeble-minded which can be made in considerable measure self-supporting. A given colony must, of course, be for one sex alone. Much can be done, furthermore, by putting into operation, both in and out of institutions, effective systems of registering births and deaths together with accompanying facts which may prove of eugenical significance.

Again, we should more surely identify and exclude undesirable immigrants and also undertake thoroughgoing investigations to determine which races we can not profitably assimilate into our own blood. Since the individual states are at the expense of maintaining in custodial institutions such defectives and degenerates as the Federal Government admits into the United States, the citizens of any particular state are well within their rights in insisting that the Federal Government select immigrants effectively or reimburse the state for its care of foreign-born defectives.

Physicians should pay more attention to the hereditary and congenital aspects of their cases and make it more a matter of conscience than they do at present to advise patients with regard to marriage. Prenuptial medical inspection should become the custom, if not by law at least as a voluntary procedure. Every parent must come to realize the grave risk to which he is subjecting his daughter if a guarantee of physical fitness, even more than assurance of financial standing or social position, is not forthcoming from her prospective mate.

Wholly apart from the field of heredity though in a realm intimately concerned with the birthright of the child, much practical good can be accomplished by pondering the facts and the fictions of prenatal influence and in the light of the knowledge thus gained, seeing that while foolish and unnecessary worries are abolished, the conditions of health, nutrition and occupation surrounding the expectant mother are the best obtainable. It is the sacred duty of every individual, moreover, to see that the maximal possibilities of his own germ-plasm are not lowered by vicious or unwholesome living.

As individuals we can cultivate a greater sense of responsibility regarding marriage and parenthood in those for whose training we are responsible. We can study this whole subject conscientiously, keep pace with new knowledge and see that other people are likewise informed. In showing an enlightened interest in the ideals of eugenics and a sympathetic approval of wholesome marriages, a sentiment toward parenthood will gradually arise which will make it seem more desirable to many worthy people than it does at present. If we are of good stock ourselves we should recognize that it is highly desirable that we give to the race at least four children. On the other hand, if we come from a strain which is eugenically undesirable we should with equal conscientiousness refrain from contributing to human misery. For where serious obstacles to a union exist, renunciation is certainly a higher manifestation of love than is consummation of a marriage which will result in untold misery to the object of the affections. As a matter of fact, with adequate preliminary knowledge as to what actually constitutes a serious drawback to marriage, where such really exists and is recognized by the associated individuals, love of the kind that leads to marriage is not likely to arise.

As has been suggested by various students of eugenics, it is even at present perhaps not infeasible for earnest individuals to start in a quiet way local centers for the keeping and filing of accurate records of their family traits for the future use of their descendants. Such groups, voluntary though they be, would soon acquire a degree of distinction that would make other people of good endowments wish to join in and go on record as eugenically desirable.

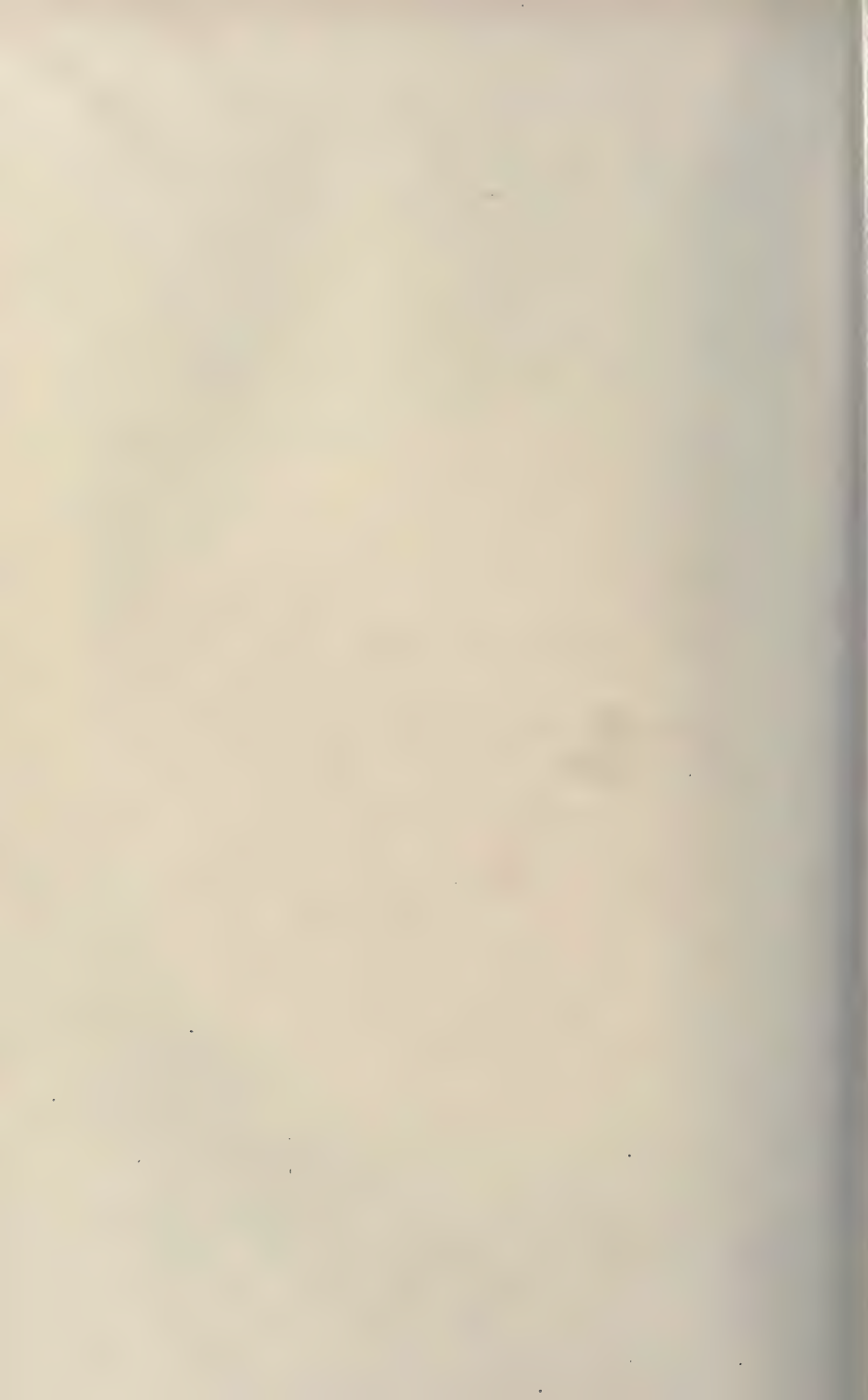
Lastly, it should not be forgotten that good traits are inherited as certainly as bad ones. Moreover, in the realm of human con-

duct, even though the fundamental features of behavior are based on an inherited organization, man is not always driven by an inexorable linkage of inherited neural units into only one line of conduct, since more or less capacity for alternative action is also inherited. It is the personal duty of every member of society to aid in affording the opportunity and providing the proper stimuli to insure that out of the many possibilities of behavior which exist in the young at birth, those forms are realized which are best worth while to the individual and to society. And while we recognize that improved environment alone can not correct human deficiencies we must nevertheless not relax our efforts to get cleaner foods, cleaner surroundings, cleaner politics and cleaner hearts.

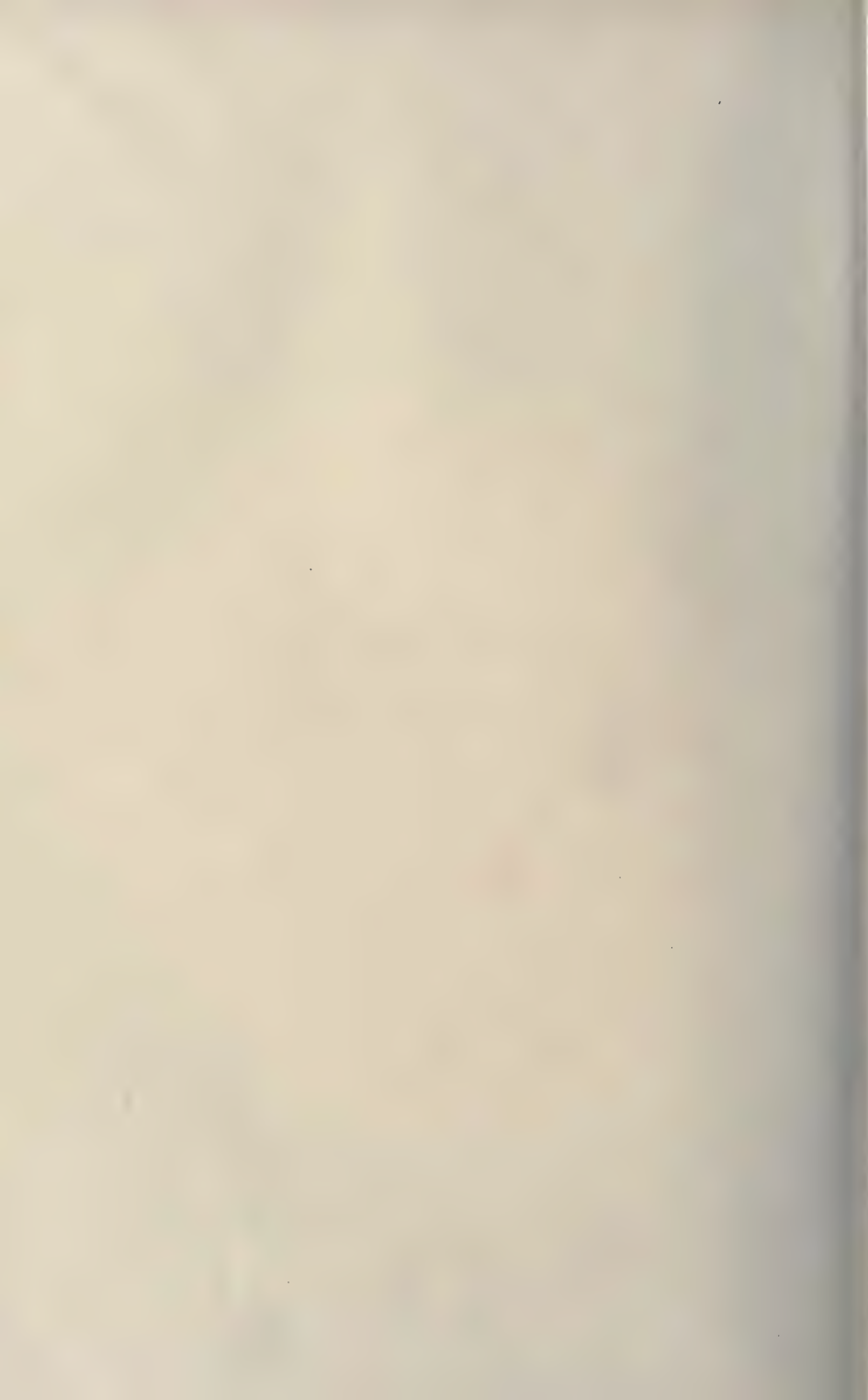
Which Shall It Be?—As a matter of social evolution, human homes originated in the necessity of an abiding place for the nurture and training of the young past their first period of helplessness. Well in the foreground of the mental picture which arises when we hear the very word *home*, are children. What shall the home of the future be with regard to its most important assets, the children? Shall we as a people continue to be confronted at every turn by the dull countenance of the imbecile, the inevitable product of a bad parental mating; or the feeble body and the clouded intellect of the child sprung from a parentage of polluted blood; or the furtive cunning of the young delinquent, the will-less mind of the born degenerate, or the shiftless spawn of the pauper? Or shall it be a type with laughing face, with bounding muscles, with unclouded brain, overflowing with health and happiness—in short, *the well-born child*?

The answer is in our own hands. The fate of many future generations is ours to determine and we are false to our trusteeship if we evade the responsibility clearly laid before us. How conscientiously we heed known facts, how actively we acquaint ourselves with new facts, and how effectively we execute the obvious duties demanded by these facts will give us the answer.

THE END



APPENDIX



APPENDIX A

BIOMETRICAL METHODS

Before glancing at various of the more important methods and formulæ used in biometrical studies it will be well to discriminate more sharply than has been done so far in certain matters of terminology.

Standard Deviation.—Two groups or populations may have the same mode and mean and yet differ widely in their spread or range of variability. In order to compare two such groups it is necessary, therefore, to have some standard expression which shows this scatter or spread above and below the group average. Mathematicians have devised for this purpose a measure of variability known as the *standard deviation*, which enables us to express the distribution of the different classes of a group of individuals (termed *variates*) about the mean. The number of individuals in a particular class are termed *frequencies* of that class; the letter f is generally used to represent the frequency in each class. Standard deviation is usually denoted by the symbol σ and its computation is ordinarily indicated by the

$$\text{formula } \sigma = \sqrt{\frac{\sum D^2 f}{n}}$$

This put into words means simply that to obtain the *standard deviation* one must square the deviation of each separate class (indicated by D) from the arithmetical mean and multiply the product by the number (indicated by f) in each class. The symbol Σ signifies that the totals thus obtained are then all to be added together. The final sum must next be divided by the total number of individuals (represented by n) in the group measured, and the square root of the whole extracted.

How this works out in an actual case is well illustrated in Table I, taken from Babcock and Clausen. The data are based on the figures of Love and Leighty showing variations in the yield of a certain variety of oats. The number of plants studied (n) was 400. The first column headed V represents the scale of measurement or, in other words, the series of class values,

here ranging by grams from 0.5 gram to 8.5 grams. The second column headed f shows what is termed the *frequency*, that is, the number of individuals in each class. For example, only 3 individuals were as light as 0.5 gram; 50 individuals fell within the 1.5 gram class, 106 in the 2.5 class, etc. The third column, headed $f.V$ represents merely the product of each class by its frequency. This knowledge once secured, then it is possible to determine the mean (M), since the mean is obtained by multiplying each class value (V) by its frequency (number of variates it contains), adding all the products together and dividing by the total number of variates (i. e. the total number of individuals concerned). In the table in question column 3 totals 1383, or briefly expressed $\Sigma (f.V) = 1383$. Since the number of variates is 400, the mean is $\frac{1383}{400}$ or 3.458. Column 4 headed d (same as D of the formula) shows the deviation of each

TABLE I.—TO COMPUTE THE STANDARD DEVIATION IN MEAN TOTAL YIELD OF PLANT IN GRAMS (Complete Process Including Calculation of the Mean). From BABCOCK AND CLAUSEN.

V	f	$f.V$	d	d^2	$f.d^2$
0.5	3	1.5	—2.958	8.750	26.250
1.5	50	75.0	—1.958	3.854	191.700
2.5	106	265.0	—0.958	0.918	97.308
3.5	109	381.5	0.042	0.002	0.218
4.5	80	360.0	1.042	1.086	86.880
5.5	42	231.0	2.042	4.170	175.140
6.5	7	45.5	3.042	9.254	64.778
7.5	2	15.0	4.042	16.338	32.676
8.5	1	8.5	5.042	25.442	25.442
	$n = 400$	$\Sigma (f.V) = 1383$ $M = 3.458$			$\Sigma (f.d^2) = 700.392$

$$\sigma = \sqrt{\frac{700.392}{400}} = 1.316.$$

class from the mean. For example, since the mean is a weight of 3.458 grams and the first class weighs only 0.5 grams, its deviation is in the minus direction and equals 2.958 (i. e. $3.458 - 0.5 = 2.958$); similarly the second (1.5 class) has a minus deviation of $3.458 - 1.5$ or 1.958; the third (2.5) class has a

minus deviation of 0.958. Beginning with the fourth (3.5) class the individuals are all heavier than the mean and the deviations are therefore all in the plus direction. Column 5 (d^2) gives the squares of the various deviations, and column 6 ($f.d^2$) shows the products of these squares by their respective frequencies (shown in column 2). This column when added gives a total of 700.392; or briefly $\Sigma(f.d^2) = 700.392$.

Supplying now the known figures in the formula $\sigma = \sqrt{\frac{\Sigma D^2 f}{n}}$

the *standard deviation* σ is found to be 1.316 (i. e. $\sigma = \sqrt{\frac{700.392}{400}} = 1.316$).

Coefficient of Variability.—While such an index of variability as standard deviation is of value in comparing two or more groups with reference to the same kind of characteristics or parts measured in like units, when comparison of unlike characteristics such as height and weight are to be made, the respective indices of variability must be converted into percentages of the different group averages. This is done by dividing the standard deviation by the mean. The quotient is called the *coefficient of variability*. For example in a certain group of men the standard deviation for weight was found to be about 16.5 pounds, and for height about 2.7 inches, but pounds and inches can not be compared. However, the *coefficients of variability* can be obtained in percentages which *can* be compared. Thus since the average height of the men in question was approximately 69 inches and the average amount of individual variation (standard deviation) was about 2.7 inches, then the percentage of variability (*coefficient of variability*) in height was about 3.9 (i. e. 2.7 equals about 3.9 per cent of 69). Similarly since the average weight was 153 pounds and the standard deviation for weight was about 16.5 pounds, the coefficient of variability for weight is approximately 10.8 per cent. Since these two coefficients (3.9 and 10.8) are both expressed in percentages, they may be compared and when this is done it is seen that this particular group of men was more than two and one-half times as variable in weight as in stature.

Construction of Correlation Tables.—Correlation tables may easily be constructed which show graphically whether or not there is correlation between two characters or activities. Such a table, from Castle, is shown in Table II, wherein the data to

be compared for possible correlation are the height and weight of one thousand college students of ages 18 to 25. Across the top of the table is the scale of height in centimeters, and in the left vertical column, the range of weights in kilograms. The height and weight of each individual is entered in the square in which the column representing his height and the row representing his weight intersect. For example (see Table II, below) there were twenty-five individuals of 173 to 175 centimeters in height who weighed from 65 to 67 kilograms; there were two

TABLE II.—SHOWING THE VARIATION IN HEIGHT AND WEIGHT AND THE CORRELATION BETWEEN HEIGHT AND WEIGHT AMONG 1000 HARVARD STUDENTS OF AGES 18-25 MEASURED AT THE HARVARD GYMNASIUM IN THE YEARS 1914-1916. CASTLE:
GENETICS AND EUGENICS.

Weight in Kilos.	Height in Centimeters																To- tals
	155- 157	158- 160	161- 163	164- 166	167- 169	170- 172	173- 175	176- 178	179- 181	182- 184	185- 187	188- 190	191- 193	194- 196	197- 199		
44- 46	---	---	I	---	---	---	---	---	---	---	---	---	---	---	---	I	
47- 49	I	---	3	I	---	---	---	---	---	---	---	---	---	---	---	5	
50- 52	I	2	I	6	4	6	2	---	---	---	---	---	---	---	---	22	
53- 55	I	4	8	15	12	8	7	2	---	---	I	---	---	---	---	58	
56- 58	---	I	4	10	15	19	20	11	3	2	---	---	---	---	---	85	
59- 61	---	I	5	8	22	43	25	21	11	4	2	---	---	---	---	142	
62- 64	I	---	2	8	9	31	39	29	21	10	2	2	---	---	---	154	
65- 67	---	---	I	2	10	21	25	39	30	18	4	---	I	---	---	151	
68- 70	---	---	I	I	9	6	30	27	32	16	13	2	---	I	---	138	
71- 73	---	---	---	2	4	5	18	20	12	18	15	4	2	---	---	100	
74- 76	---	---	---	---	I	4	11	15	6	7	9	6	---	---	I	60	
77- 79	---	---	---	---	I	2	2	8	5	7	4	4	I	---	---	34	
80- 82	---	---	---	---	---	---	4	6	3	4	6	2	---	---	---	25	
83- 85	---	---	---	---	---	---	2	I	2	3	2	2	---	---	---	12	
86- 88	---	---	---	---	2	I	2	---	---	2	---	---	---	---	---	7	
89- 91	---	---	---	---	---	---	---	---	---	I	I	---	---	---	---	2	
92- 94	---	---	---	---	---	---	I	I	---	---	---	---	---	---	---	2	
95- 97	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
98-100	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
101-103	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
104-106	---	---	---	---	---	---	---	I	---	---	I	---	---	---	---	2	
Totals	4	8	26	53	89	146	188	181	125	92	60	22	4	I	I	1000	

Mean height = 174.4 cm. (5 ft. 8.4 in.)

Mean weight = 65.9 kilos. (145.28 lbs.)

σ height = 6.56 cm.

σ weight = 11.9 kilos.

$C V$ height = 3.8%

$C V$ weight = 11.9%

r height-weight = .54

of this same height who weighed only 50 to 52 kilograms; 7 who weighed 53-55 kilograms, et cetera. When all the observations have thus been tabulated the table will show the extent to which men vary in weight as they vary in height. The degree to which the individuals group themselves about a diagonal ranging from upper left- to lower right-hand corner indicates the relative amount of correlation between the two things being measured. Complete correlation would be represented by a single series of squares along this diagonal. On the other hand inverse or negative correlation would be shown by a grouping of the entries in the table about a diagonal running from the upper right- to the lower left-hand corner. If there were no correlation the measurements would be distributed at random over the entire table. In the particular table used for illustration the correlation is fairly high.

The Coefficient of Correlation.—Ordinarily the degree of correlation is expressed in the form of a “coefficient of correlation.” This coefficient is commonly indicated by the letter r and it is calculated by the formula:
$$r = \frac{\sum D_x D_y f}{n \sigma_x \sigma_y}.$$

Although this formula may look a bit terrifying to the mathematically untrained, the computations called for are relatively simple. The x and y merely represent the two objects or conditions being compared; or in other words, x is one variable and y the other. In the present illustration x stands for height, y for weight. The symbol σ represents standard deviation and the method of determining this has already been explained (p. 447). The expression $\sigma_x \sigma_y$, therefore, indicates that the standard deviation of x (i. e. of height) is to be multiplied by the standard deviation of y (i. e. of weight). The letter D , as in the formula on page 442 represents the deviation of each separate class from the mean, and the expression D_x , therefore, simply means the deviations for height (x), and D_y , the deviations for weight (y). Σ is the summation sign which shows that the sum of the products indicated are all to be added together. The letter n , as usual, indicates the total number of individuals obtained. When the proper numerical quantities are substituted for the symbols in the equation, the coefficient of correlation for height (x) and weight (y) of the thousand students studied, is found to be 0.54. As indicated at the bottom of the table the mean height was 174.4 cm. (5 ft. 8.4 in.), the mean weight 65.9 kilos. (145.28

lbs.); the standard deviation for height (x) was 6.56 cm., for weight, 11.9 kilos; the *coefficient of variation* (obtained by dividing standard deviations by the mean) for height is 3.8 per cent., and for weight, 11.9 per cent.; and the *coefficient of correlation* (r) between height and weight is 0.54.

In general, a coefficient of as low as 0.10 is regarded as not showing significant relation; 0.10 to 0.25 is slight though appreciable; 0.25 to 0.50 is moderate; 0.50 to 0.75 shows a marked relation; 0.75 to 0.90 is very high; and 1.00, of course, shows complete correlation.

Probable Error.—Finally there must be some check on the reliability of statistical conclusions. It is obvious, for example, that if in "random sampling" only a small number of individuals were taken as representative of a large population there is much greater chance of the sample not being a fair one than if large numbers of individuals were taken. In other words, a mathematical expression is needed to indicate the probable accuracy of biometrical measurements or conclusions. This is met by calculating what is called the "probable error."

The theory of error is a generalization of the laws of probability or chance, and the "probable error" expresses the amount that must be added to or subtracted from the statistically calculated value to obtain two limits (plus and minus) within or without which there is equal chance that the true value lies. For example, in studying the inheritance of scale numbers in the banded region of the nine-banded armadillo, Newman calculated the standard deviation of 508 individuals to be 14.89 ± 0.31 . In other words the standard deviation from the mean was about 14.89 scales with a probable error of ± 0.31 . That is, the figure 14.89 may be inaccurate to the extent of being 0.31 scales too high or too low.

For our purpose it is unnecessary to go into the mathematical derivation of the method for determining the probable error of any calculated constant—this would lead us far afield into mathematical theory. We shall have to rest content with seeing why such corrections are necessary, the nature of the facts upon which they are based, and the presentation of the formulæ for calculating the probable error of the constants most commonly used in biometry. The symbols in the following equations have the same meaning as in those given earlier in this discussion. It is a simple matter to make the necessary arithmetical substitutions and calculate the result thus:

The *probable error* of the *mean* (E_m) is represented by the formula $E_m = \pm \frac{0.6745 \sigma}{\sqrt{n}}$ which being interpreted simply means that the probable error of the mean is found by multiplying the standard deviation (σ) by 0.6745 and dividing by the square root of the number of individuals involved in the calculation. Similarly the *probable error* of the *standard deviation* is expressed by the equation $E\sigma = \pm 0.6745 \frac{\sigma}{\sqrt{2n}}$; that for the *coefficient of variability*, by the formula $E_c = \pm 0.6745 \frac{CV}{\sqrt{2n}}$; and the *probable error* of the *coefficient of correlation*, by the equation $E_r = \frac{\pm 0.6745 (1 - r^2)}{\sqrt{n}}$.

In comparing two sets of statistical results where there is a difference, the probable error of this difference is found by extracting the square root of the sum of the squares of the probable errors of the two results. Unless the actual difference between the constants of the two sets is at least from 3 to 3.5 as great as this probable error, the difference is not regarded as significant.

The Short Method.—Much of the labor involved in calculating statistical coefficients is due to the fractions involved. To simplify such computation a so-called "short method" has been devised. Instead of the true mean which so frequently ends in a lengthy fraction, a mean (conveniently near the true mean) which is a whole number or one involving but one decimal place is assumed. This assumed mean is used in all computation as if it were the true mean and then at the conclusion a correction (c) is made for the amount by which the assumed mean differs from the true mean. The correction is found by the formula

$c = \frac{Df}{n}$ in which D is the deviation (in whole numbers) of

each class from the *assumed* mean, regard being given to sign, and f and n , as usual, indicate frequency and total number of variates respectively. To get the true mean the numerical value of c is added to or subtracted from the assumed mean, as the case may be. The short method formula for the *standard deviation* is

$$\sigma = \frac{D^2 f}{n} - c^2$$

in which D represents deviation from the assumed mean, c signifies the correction which must be made in the assumed mean to get the true mean, and the other symbols have their usual meaning. The short method formula for the *coefficient of correlation* is

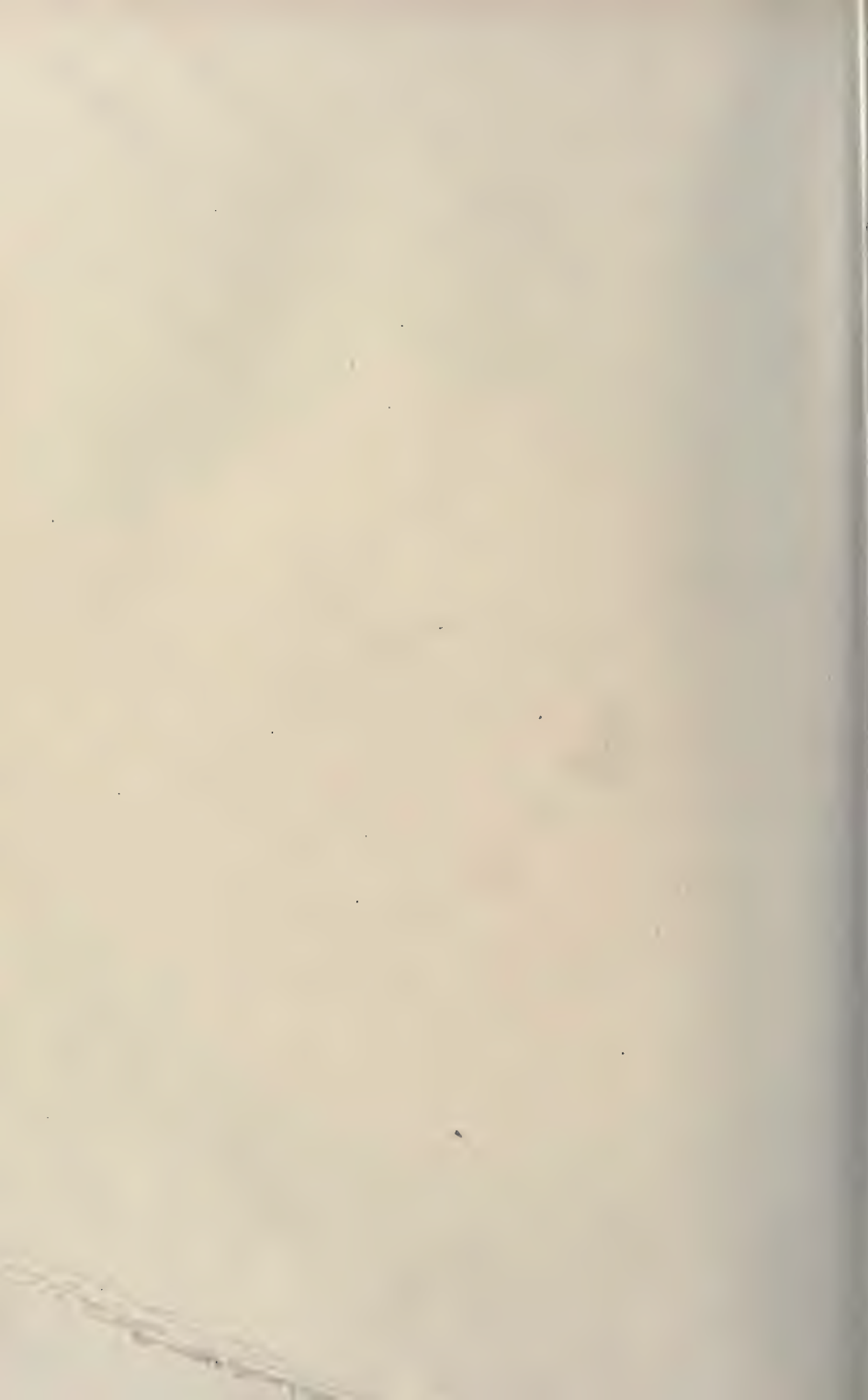
$$r = \left(\frac{\sum D_x D_y f}{n} - c_x c_y \right) \frac{1}{\sigma_x \sigma_y}$$

in which x and y indicate merely the characters between which possible correlation is being sought, and the other symbols have the same significance as in the preceding formula for standard deviation. (Also see Harris, *American Naturalist*, Vol. 44, 1910.)

For more detailed descriptions of biometrical methods and for various short-cuts by which certain of the calculations may be simplified, the reader must be referred to such special books as (1) Davenport, C. B.: *Statistical Methods with Special Reference to Biological Variation*; (2) Davenport, E.: *Principles of Breeding*; (3) Yule, G. U.: *An Introduction to the Study of Statistics*; (4) King, W. I.: *Elements of Statistical Methods*; (5) Elderton: *Primer of Statistics*; (6) Pearl, R.: *Introduction to Medical Biometry and Statistics*; (7) Jones, D. C.: *A First Course in Statistics*. The student who wishes to try his hand at actual biometrical work in genetics will find a valuable chapter (Chapter III) on practical procedure in Babcock and Clausen: *Genetics in Relation to Agriculture*.

A pamphlet entitled *Correlation and Machine Calculation*, by Wallace and Snedecor, published by Iowa State College, at Ames, Iowa, giving explicit directions for the use of commercial forms of calculating machines in finding correlation, coefficients or related constants, will be found helpful in practical work.

GLOSSARY



GLOSSARY

- ACHROMATIN (Gr. *chroma*, color), the non-staining substance of the nucleus as contrasted with the chromatin.
- ACQUIRED CHARACTERS, traits developed in the body through changes in environment or function, in contra-distinction to those which have their specific causes in the germ-cells.
- ADAPTATION (L. *ad*, to; *aptus*, fit), fitness to environment.
- ADRENAL BODY (L. *ad*, near; *ren*, kidney), a small body on the upper side of the kidney.
- AGGLUTINATION (L. *agglutinans*, gluing), collection, into clumps, of cells distributed in a fluid; supposedly caused by specific substances called agglutinins found in the blood as the result of infection or the introduction of the foreign cells for which they are specific.
- ALBINISM (L. *albus*, white), a condition of deficiency in pigment.
- ALLELOMORPH (Gr. *allelon*, of one another; *morphē*, form), one of a pair of alternate Mendelian characters.
- AMEBA (Gr. *amoibē*, change), a primitive single-celled animal.
- AMNION (Gr. *amnos*, lamb), the innermost membrane that incloses the fetus, forming the "bag of waters."
- AMPHIBIAN (Gr. *amphi*, both; *bios*, life), capable of living both on land and in water.
- ANTHROPOID (Gr. *anthropos*, man; *eidōs*, form), manlike.
- ANTIBODY, a substance engendered in the blood and tissue juices of animals by the introduction into the blood stream of bacterial protein products or other foreign proteins. An antibody exerts a specific antagonistic influence on the substance (known as *antigen*) under the influence of which it was formed.
- ANTIGEN (Gr. *anti*, against; *gen*, to form), a substance which causes the formation of antibodies.
- ANTITOXIN (Gr. *anti*, against; *toxikon*, poison), a defensive substance in the body, either existing there naturally or developed as a result of the invasion of a poison which it tends to neutralize.

- AORTA** (Gr. *aorta*, raise), the large main artery springing from the heart.
- ARISTOGENIC** (Gr. *aristos*, best; *genesis*, origin), pertaining to the genetically most desirable human strains.
- ASSOCIATION AREAS**, those regions of the brain in which presumably the higher mental processes are effected.
- ATAVISM** (L. *ad*, before; *avus*, grandfather), a return in one or more characters to an ancestral type. See pp. 5, 6 for restricted modern usage.
- ATROPHY** (Gr. *a*, negative; *trophē*, nourishment), a wasting away of a part of a living organism.
- AXON** (Gr. *axon*, axis), the process from a nerve cell which becomes a nerve fiber.
- BACK CROSS**, a mating between an F_1 hybrid and one of its parent types; also applied to the offspring of such a cross.
- BINET-SIMON SCALE**, a series of tests graded to age and previous training of the average normal child, much used in measuring mental deficiency.
- BIOLOGY** (Gr. *bios*, life; *logos*, discourse), the study of life and of living things.
- BIOMETRY** (Gr. *bios*, life; *metron*, measure), the study of biological problems by means of statistical methods.
- BIOTYPE** (Gr. *bios*, life; *typos*, type), a group of individuals all of which have the same genotype.
- BLASTOCÆLE** (Gr. *blastos*, germ; *koiolos*, hollow), the cavity within a blastula.
- BLASTOMERE** (Gr. *blastos*, germ; *meros*, part), one of the early cells formed by the division of the ovum.
- BLASTOPHTHORIA** (Gr. *blastos*, germ; *phtheiro*, destroy), deterioration of the germ as the result of direct pathogenic or other disturbing agents.
- BLASTOPORE** (Gr. *blastos*, germ), the mouth-like opening of a blastula.
- BLASTULA** (Gr. *blastos*, germ), a mass of cells, usually in the shape of a hollow sphere, resulting from the cleavage of an egg.
- BLENDING INHERITANCE**, inheritance in which the characters of the parents seem to blend in the offspring.
- CACOGENIC** (Gr. *kakos*, bad; *genesis*, origin), pertaining to genetically undesirable human strains.
- CELL**, the fundamental unit of structure in plants and animals.

- CENTROSOME (Gr. *kentron*, center; *soma*, body), a small body which functions in indirect cell division.
- CEREBRUM (L. *cerebrum*, brain) the anterior (in man upper) part of the brain consisting of two hemispherical masses; often termed the hemispheres.
- CHARACTER, any distinguishing feature, trait or property of an organism.
- CHEMOTROPISM (chemical and tropism), defined, p. 309.
- CHORION (Gr. *chorion*, membrane), the more external of the two fetal membranes.
- CHROMATIN (Gr. *chroma*, color), deeply staining substance of the cell-nucleus.
- CHROMOMERES (Gr. *chroma*, color; *meros*, part), the linear series of chromatin bodies in a chromosome.
- CHROMOSOMES (Gr. *chroma*, color; *soma*, body), characteristic deeply staining bodies, typically constant in number and appearance in each species of animal or plant, which appear in the cell during indirect division.
- CHROMOTROPISM (Gr. *chroma*, color; *tropē*, turning), defined, p. 309.
- CILIA (L. *cilium*, eyelid), minute vibratile hair-like processes attached to a free cell-surface. Often arranged in rows suggesting eyelashes, hence the derivation.
- CLEAVAGE, the division of the egg-cell into many cells.
- CÆLOM (Gr. *koilos*, hollow), the body-cavity.
- COMPLEMENTARY FACTORS, see page 159.
- CONGENITAL (L., *con*, together; *gigno*, bear), present at birth.
- CONJUGATION (L. *con*, together; *jugum*, yolk), the union of germ-cells or unicellular individuals for reproduction.
- CONSTRUCTIVE (or positive) EUGENICS, a system of securing a superior race through propagation of the fittest individuals.
- CONTINUOUS VARIATION, a finely graded series of minute variations fluctuating about a mean.
- CORRELATION, mutual or reciprocal relation between two quantities or parts.
- CORTEX (L. *cortex*, bark), outer or investing layer of the brain.
- CRISSCROSS INHERITANCE, inheritance in which maternal characters are transmitted to sons and paternal characters to daughters.
- CROSSING OVER, the regrouping of linked characters, probably caused by the exchange of genes between homologous chromosomes during synapsis.

- CYCLOPIA (Gr. *kyklos*, circle; *ops*, eye), a monstrosity in which the two eyes have fused into a single one.
- CYTOLOGY (Gr. *kytos*, hollow place, cell), the science which treats of cells.
- CYTOLYSIN (Gr. *kytos*, hollow place; *lysis*, dissolution) a substance which produces dissolution of cells.
- CYTOPLASM (Gr. *kytos*, cell; *plasso*, form), the protoplasm of the cell outside of the nucleus.
- CYTOTOXIN (Gr. *kytos*; *toxikon*, poison), a substance which has a specific toxic action upon cells or special organs.
- DALTONISM, the commonest form of color-blindness in which the affected individual is unable to discriminate between red and green.
- DENDRITES (Gr. *dendron*, tree), branching processes which spring from nerve-cells.
- DETERMINER (L. *determinare*, to determine), the distinctive cause or unit in a germ-cell which determines the development of a particular character in the individual derived from that cell. The terms *gene* and *factor* are sometimes used as synonyms of determiner.
- DIFFERENTIATION, the specializing process whereby specific parts or substances are formed in living organisms.
- DIHYBRIDS (L. *di*, two; *hybrida*, mongrel), the offspring of parents differing in two characters.
- DIOECIOUS PLANT (Gr. *di*, two; *oikos*, house), a plant having the male and female organs in separate individuals.
- DIPLOID (Gr. *diploos*, double; *eidōs*, form), the dual or somatic number of chromosomes.
- DOMINANT CHARACTER (L. *dominare*, to be a master), a character from one parent which manifests itself in offspring to the exclusion of a contrasted character from the other parent.
- DROSOPHILA, a genus of fruit flies of which there are several species.
- DUPLEX (L. *duo*, two; *plico*, fold), the condition in which a character is represented by two determiners, one from each parent.
- DUPLICATE FACTORS, different sets of factors having identical though not cumulative effects.
- ELECTROTROPISM (Gr. *electron*, amber; *tropē*, turning), defined, p. 309.

- EMBRYO (Gr. *embryon*), the young organism in its earliest stages of development.
- EMBRYOGENY (Gr. *embryon*; *genesis*, generation), the development of the embryo.
- ENDOCRINE (Gr. *endon*, within; *krinein*, to separate) pertaining to internal secretions derived directly from a gland by the blood.
- ENDODERM (Gr. *endon*, within; *derma*, skin), the inner cell-layer of an embryo.
- EQUATION DIVISION, the usual nuclear division in which each chromosome divides equally.
- EUGENICS (Gr. *eugenes*, well-born), the science relating to improvement of the human race through good breeding.
- FACTOR, a specific germinal cause of a hereditary character. See determiner.
- F₁, F₂, etc., first filial, etc., indicating the successive generations following a cross.
- FEEBLE-MINDEDNESS, deficiency in mental development. For grades, see p. 334.
- FERTILIZATION, union of the sexual cells.
- FETUS (L. *fevere*, to bring forth), the unborn young animal in its later (after second month in man) stages of development.
- FISSION, division into two equal parts in asexual reproduction.
- FLAGELLUM (L. *flagellum*, little whip), a vibratile, thread-like organ of locomotion.
- FLUCTUATING VARIATIONS, variations which deviate from one another very slightly.
- FOREIGN PROTEIN, a term used in immunology for a protein not belonging to the animal (or generally the *kind* of animal) under experimentation.
- FRATERNAL TWINS, twins produced from different eggs, and showing different hereditary characters.
- GAMETE (Gr. *gamos*, marriage), a mature germ-cell.
- GAMETOPHYTE (Gr. *gamos*, marriage; *phyton*, plant), that phase of a non-flowering plant which produces the sex-cells.
- GASTRULA (Gr. *gaster*, belly), a stage in embryonic development in which the embryo consists of an outer (ectoderm) and an inner (endoderm) layer of cells, enclosing a cavity (archenteron) and having an opening (blastopore) at one end.
- GENE (Gr. *gen*, to form), a specific germinal cause of a hereditary character. See determiner.

- GENETICS (Gr. *genesis*, origin), the science which deals with heredity and the origin of individuals in general.
- GENOTYPE (Gr. *genea*, race; *typto*, strike), the germinal constitution of an organism.
- GEOTROPISM (Gr. *ge*, earth; *tropē*, turning), defined, p. 309.
- GERM-CELL, a reproductive cell.
- GERMINAL VARIATIONS, variations which owe their origin to some modification in the germ-cells.
- GERM-PLASM, the material basis of inheritance.
- GONAD (Gr. *gonos*, generation), a germ-gland.
- HAPLOID (Gr. *haploos*, single; *eidos*, form), the single or reduced number of chromosomes as found, for instance, in the mature germ-cells.
- HELIOTROPISM (Gr. *helios*, sun; *tropē*, turning), defined, p. 309.
- HEREDITY (L. *heres*, heir), resemblance of individuals to their progenitors based on community of origin.
- HERITAGE (L. *heres*, heir), all that is inherited by an individual.
- HETEROMORPHOSIS (Gr. *heteros*, other; *morphē*, form), development of a part different from the one removed in regeneration phenomena.
- HETEROSIS (Gr. *heteros*, other, different), increased vigor due to hybridism.
- HETEROZYGOSIS, cross-breeding, hybridization. See heterozygote.
- HETEROZYGOTE (Gr. *heteros*, others; *zeugon*, yolk), an individual produced through the union of germ-cells which are unlike in determiners. Adjective, *heterozygous*.
- HOMOLOGOUS CHROMOSOMES (Gr. *homos*, same; *lego*, speak), pairs of chromosomes having relatively similar structure and value of the chromosome complex; one comes from each parent.
- HOMOZYGOTE (Gr. *homos*, same; *zeugon*, yolk), an individual produced through the union of germ-cells which are alike in determiners. Adjective, *homozygous*.
- HYBRID (L. *hybrida*, mongrel), the offspring of parents which differ in one or more characters.
- IDENTICAL TWINS, twins which show identical inborn characters, both having come presumably from the same ovum.
- IDIOT (Gr. *idios*, peculiar, private), defined, p. 334.
- IMBECILE (L. *imbecillis*, weak), defined, p. 334.
- IMMUNIZATION (L. *immunis*, safe), the process of rendering a
immune to certain diseases or to the effects of foreign
introduced into the blood stream.

- INDUCTION (L. *in*, in; *duco*, lead), modification of first generation offspring caused by environmental action on the parental germ cell; *parallel induction* consists in simultaneous modification of soma and germ by an environmental agent.
- INHERITANCE (L. *in*, in; *heres*, heir), the sum of all characters which are transmitted by the germ-cells from generation to generation.
- INHIBITOR (L. *in*, in; *habeo*, hold, have), that which checks or restrains.
- INSTINCT (L. *in*, in; *stingno*, prick), defined, p. 313.
- INTERSEX, an individual displaying characters of each sex.
- INTRA-UTERINE (L. *intra*, within; *uterus*, the womb), within the womb.
- IRRITABILITY (L. *irrito*, excite), the capacity of responding to stimuli.
- LAMARCKISM, the doctrine of Lamarck that evolution takes place through the inheritance of somatic acquirements.
- LETHAL FACTOR (L. *lethum*, death), a factor which causes the early death of the germ or the zygote.
- LININ (L. *linum*, flax), filaments of the cell-nucleus not readily stained by dyes.
- LINKAGE, inheritance of characters in groups, probably due to the fact that their genes lie in the same chromosome.
- LUETIN TEST (L. *lues*, pest), a test for syphilis; see p. 298.
- MAMMALS (L. *mamma*, breast), warm-blooded, hairy animals which suckle their young.
- MATURATION (L. *maturus*, ripe), the final stages in the development of the sex-cells characterized by two divisions in one of which the number of chromosomes is reduced by one-half.
- MEAN, a quantity having an intermediate value in a series of quantities or between two extremes; the average, or arithmetic mean.
- MENDELIAN, MENDELISM, referring to Mendel, the founder of a theory of heredity. See p. 127.
- MESODERM (Gr. *mesos*, middle; *derma*, skin), a layer (commonly double) or group of embryonic cells lying between ectoderm and endoderm.
- METABOLISM (Gr. *metabolos*, changeable), the sum of the constructive processes (*anabolism*) and destructive processes (*katabolism*) which go on in living matter.
- METAZOA (Gr. *meta*, over; *zoon*, animals), all than the protozoa.

MITOSIS (Gr. *mítos*, thread), indirect nuclear division, characterized by the appearance of a fibrous spindle and a definite number of chromosomes. The latter split to form daughter chromosomes which diverge to the poles of the spindle to form parts of the new nuclei.

MODIFYING FACTORS, factors which modify other factors or the characters to which they give rise.

MONGOLIAN, a type of feeble-minded individual, see p. 351.

MONOHYBRID (Gr. *monos*, single; L. *hybrida*, mongrel), the offspring of parents differing in one character.

MORON (Gr. *moros*, foolish), defined, p. 334.

MORPHALLAXIS (Gr. *morphē*, form; *allasso*, make otherwise) regeneration involving a transformation of an older part or parts of an organism into a new organism.

MULTIPLE EMBRYOS, two or more embryos derived from a single egg.

MULTIPLE FACTORS, two or more sets of factors having similar and cumulative effect.

MUTANT (L. *mutō*, change), a variant or sport which arises abruptly and breeds true.

MUTATIONS (L. *mutare*, to change), abrupt, inheritable germinal variations. Frequently though not necessarily they are changes of considerable extent.

NATURAL SELECTION, the elimination of less fit individuals in the effort to live.

NEURAL (Gr. *neuron*, nerve), pertaining to the nervous system.

NEURAL GROOVE (Gr. *neuron*, nerve), a groove along the dorsal surface of a vertebrate embryo which develops into brain and spinal cord.

NEURAL TUBE, the tube formed from the neural groove.

NEURON (Gr. *neuron*, nerve), a nerve-unit consisting of a nerve-cell with branching processes called dendrites and an axon or axis cylinder process which gives rise to a nerve fiber.

NEUROPATHIC (Gr. *neuron*, nerve; *pathos*, suffering), relating to disease of the nervous system.

NON-DISJUNCTION, failure of daughter chromosomes to separate in cell division with the result that both go to the same cell; particularly failure of maternal and paternal chromosomes to separate in the reduction division of maturation.

NOTOCHORD (Gr. *notos*, back; *chordē*, string), a rod of cells at the beginning of the back-bone in vertebrate

- NUCLEOLUS (L. dim. of nucleus), a well-defined body found within the nucleus of a cell.
- NUCLEUS (L. *nux*, a nut), the central organ of a cell.
- NULLIPLEX (L. *nullus*, not any; *plico*, fold), the condition in which no determiners of a given character exist in a particular individual.
- ONTOGENY (Gr. *on*, being; *gen*, become), the development of the individual.
- OÖCYTE (Gr. *ōon*, egg; *kytos*, cell), the ovarian egg in one stage of development.
- OÖGENESIS (Gr. *ōon*, egg; *genesis*, origin), the development of ova from primitive sex-cells.
- OÖGONIUM (Gr. *ōon*, egg; *gonos*, generation), a primordial egg-cell.
- OÖSPERM (Gr. *ōōn*, egg; *sperma*, seed), the fertilized egg.
- ORGANOGENY (Gr. *organon*, organ; *gen*, become), the formation of the organs of the body.
- ORTHOGENESIS (Gr. *orthos*, straight; *genesis*, origin) definitely directed evolution; variation in progressive sequence.
- OVARY (L. *ovum*, egg), the organ in which the egg-cells multiply and are nourished.
- OVUM (L. *ovum*, an egg), the female sex cell.
- PARTHENOGENESIS (Gr. *parthenos*, virgin; *genesis*, origin), development of an egg which has not united with a male gamete.
- PARTICULATE INHERITANCE, inheritance in which certain characters are derived from one parent, others from the other parent; Galton's term for what would now be called Mendelian inheritance.
- PATHOLOGY (Gr. *pathos*, suffer), the science which treats of disease in all its manifestations.
- PHENOTYPE (Gr. *phaino*, show; *typto*, strike), the existing type of individual irrespective of hereditary possibilities which may reside in it undeveloped.
- PHOTOTROPISM (Gr. *phos*, light; *tropē*, turning), defined, p. 309.
- PHYLOGENY (Gr. *phylon*, race, branch; *gen*, become), the development (evolution) of a group.
- PLACENTA (L. *placenta*, a flat cake), the organ by which the fetus of the higher mammals is attached to the uterine wall of the mother for purposes of nourishment, respiration and excretion. In it the maternal and fetal blood, alth^o intermingling, are brought into such close proximity that interchange of dissolved substances is -

- POLAR BODIES**, the minute cells which are separated from the egg in its maturation divisions.
- POLARITY**, having two poles of different physiological value; in the ovum there is an animal (formative) and a vegetal (nutritive) pole.
- PREPOTENCY** (L. *prae*, before; *potis*, able), preponderant capacity of one parent to transmit characteristics to the offspring.
- PRIMATE** (L. *primus*, first), the highest order of animals, including monkeys, apes and man.
- PRIMORDIAL GERM-CELLS**, the primitive sex-cells.
- PROBABLE ERROR**, a measure of the reliability of a quantitative result.
- PRONUCLEUS**, the nucleus of the mature ovum or sperm-cell.
- PROPOSITUS** (L. *propositus*, proposed), the individual from whom a family relationship is reckoned.
- PROTEIN** (Gr. *protos*, first), one of a class of highly complex compounds containing carbon, oxygen, hydrogen and nitrogen; the phenomena of life occur only in their presence.
- PROTOPLASM** (Gr. *protos*, first; *plasma*, form), the essential living substance.
- PROTOZOA** (Gr. *protos*, first; *zoon*, animals), single-celled animals or animals composed of cells not separable into different tissues.
- PSYCHICAL** (Gr. *psyche*, the soul), pertaining to the mind.
- RACE**, a group of individuals, having many similar characters due to common descent.
- RECESSIVE CHARACTER** (L. *recessus*, a going back), a character from one parent which remains undeveloped in offspring when associated with the corresponding dominant character from the other parent.
- RECIPROCAL CROSS**, a cross in which, with reference to another cross, the male is of the variety of the female and the female that of the male, of the other cross; for example, a cross of a Shorthorn bull by a Holstein cow is the reciprocal of a cross of a Holstein bull by a Shorthorn cow.
- REDUCTION DIVISION**, a division of the maturing germ-cells in which the dual or somatic (diploid) number of chromosomes is reduced to the single (haploid) number.
- REFLEX ACTION** (L. *re*, back; *flectere*, bend), an automatic response of the nervous and motor mechanism of the body.
- SELECTION** (Gr. *negatives*) **EUGENICS**, a system of improving the race by preventing reproduction of the unfit.

- REVERSION (L. *re*, back; *verto*, turn), the reappearance of ancestral traits which have for some generations been in abeyance.
- RHEOTROPISM (Gr. *rhéo*, to flow; *tropē*, turning), defined, p. 309.
- SALPINGECTOMY (Gr. *salpinx*, trumpet; *ectomē*, cutting out), removal of part or all of a Fallopian tube (oviduct).
- SECONDARY SEXUAL CHARACTERS, characters distinguishing one sex from the other but which do not function directly in reproduction.
- SEGREGATION (L. *se*, aside; *grex*, flock), separation.
- SEX CHROMOSOME, a special chromosome which is supposed to be concerned in the determination of sex.
- SEX-LIMITED CHARACTER, a character belonging to one sex only; commonly a secondary sexual character.
- SEX-LINKED CHARACTER, a character the determiner of which is located in the sex-chromosome.
- SIBLINGS, SIBS (As, *sib*, kin), offspring of the same parents.
- SIMIAN (L. *simia*, ape), ape-like.
- SIMPLEX (L. *sim*, same; *plico*, fold), the condition in which a character is represented by a determiner from only one of the two parents.
- SOMA (Gr. *soma*, body), the body considered apart from the germ-cells.
- SPERMATID (Gr. *sperma*, seed), a cell resulting from the last division of the germ-cell in spermatogenesis. It transforms into the spermatozoon.
- SPERMATOCYTES (Gr. *sperma*, seed; *kytos*, cell), cells concerned in the maturation divisions of the male germ-cells.
- SPERMATOGENESIS (Gr. *sperma*, seed; *genesis*, origin), the development of spermatozoa from primitive sex-cells.
- SPERMATOGONIUM (Gr. *sperma*, seed; *gonos*, generation), a primordial sperm-cell.
- SPERMATOZOON (Gr. *sperma*, seed; *zoon*, animal), the functional male sex-cell.
- SPINDLE, a fibrous organ formed in indirect cell-division.
- SPIREME (L. *spira*, coil), a characteristic stage preliminary to indirect cell-division in which the chromatin material of the nucleus appears in the form of a skein of filaments.
- STANDARD DEVIATION, a measure of the variability of a group.
- STEREOTROPISM (Gr. *stereos*, solid; *tropē*, turning), defined, p. 309.
- STERILIZATION (L. *sterilis*, barren), deprivation of reproductive power. For methods, see p. 432.

SUPPLEMENTARY FACTORS, see page 156.

SUPRARENAL, see adrenal.

SYNAPSE (Gr. *syn*, together; *hapto*, unite), the coming in contact of the processes of one nerve-cell with the processes or body of another.

SYNAPSIS (Gr. *syn*, together; *hapto*, unite), union of the chromosomes in pairs preliminary to the reduction division.

TELEGONY (Gr. *telegonos*, born far away), the supposed influence of an earlier sire on offspring born later of the same mother to a different sire.

THERMOTROPISM (Gr. *thero*, heat; *tropē*, turning), defined, p. 309.

THIGMOTROPISM (Gr. *thigmo*, touch; *tropē*, turning), defined, p. 309.

THYMUS (Gr. *thymos*, thyme), a ductless gland at the base of the neck.

THYROID (Gr. *thyreos*, large shield), a ductless gland (usually paired) in the neck region.

TOTIPOTENCE (L. *totus*, entire; *potis*, able), the capacity of a cleavage cell to give rise to an entire animal.

TOXIN (Gr. *toxicon*, poison), a poisonous compound of animal, vegetable, or bacterial origin.

TRIHYBRID, a cross involving three character-differences between the parents.

TROPISM (Gr. *tropē*, turning), the automatic directing of an organism toward or away from a source of stimulus.

UMBILICAL CORD (L. *umbilicus*, naval), the cord, composed mainly of blood-vessels and connective tissue, that unites the fetus with the mother.

UNIT-CHARACTER, a character which behaves as an indivisible unit in heredity.

VASECTOMY (L. *vas*, vessel; *ectomē*, cutting out), removal of a portion of the vas deferens (duct for conveying spermatozoa).

VESTIGIAL (L. *vestigium*, footstep), representing organs which existed once in a more developed condition.

VOLVOX (L. *volvo*, roll), a small fresh-water organism occurring in spherical colonies.

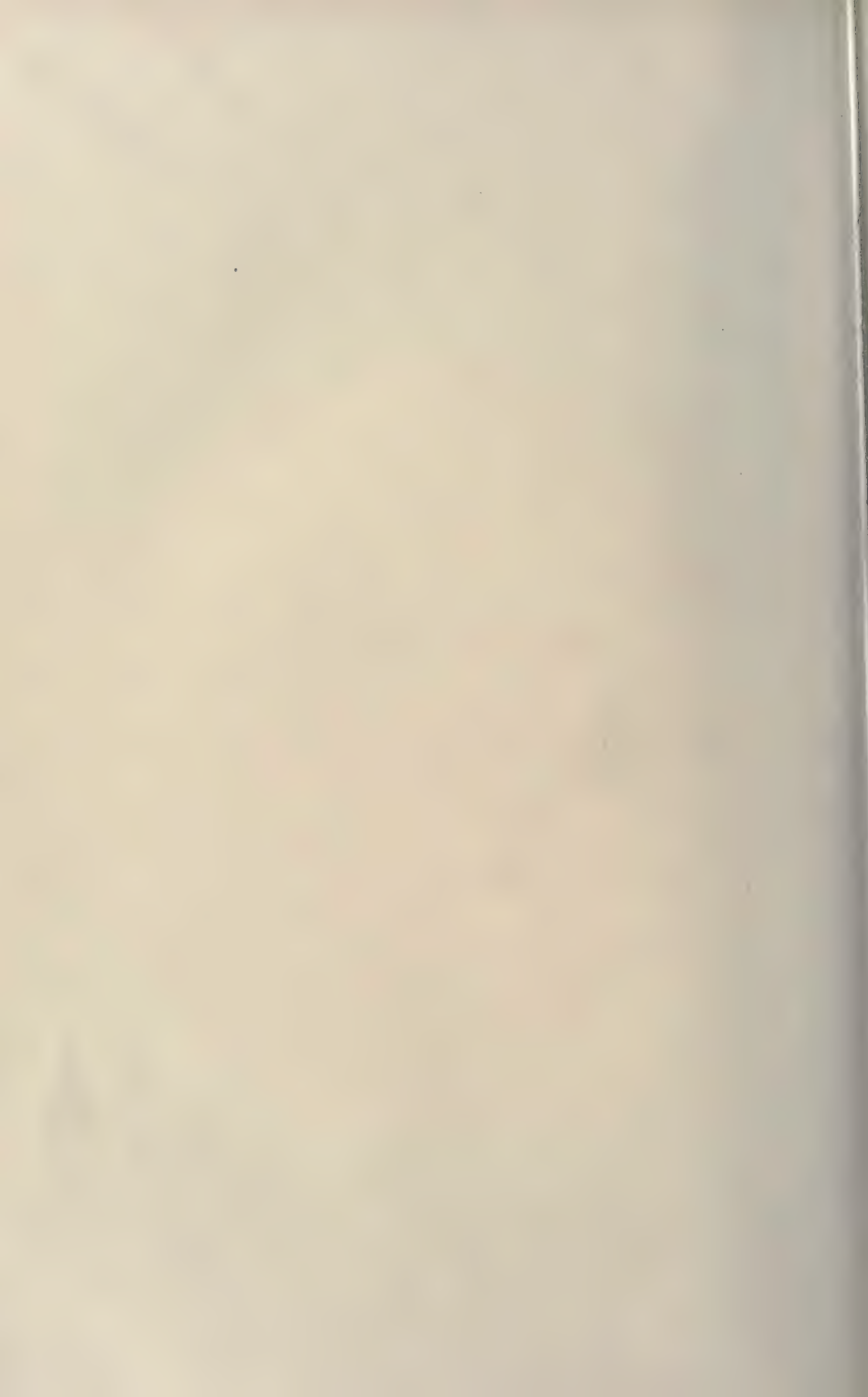
WASSERMAN REACTION, a test for syphilis, see p. 301.

X-CHROMOSOME, a chromosome associated with sex in many animals; the female has two, the male one.

Y-CHROMOSOME, a chromosome associated with sex in many animals, found normally only in the male.

ZYGOTE (Gr. *zeugon*, yolk), the product of the union of two gametes.

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REFERENCES

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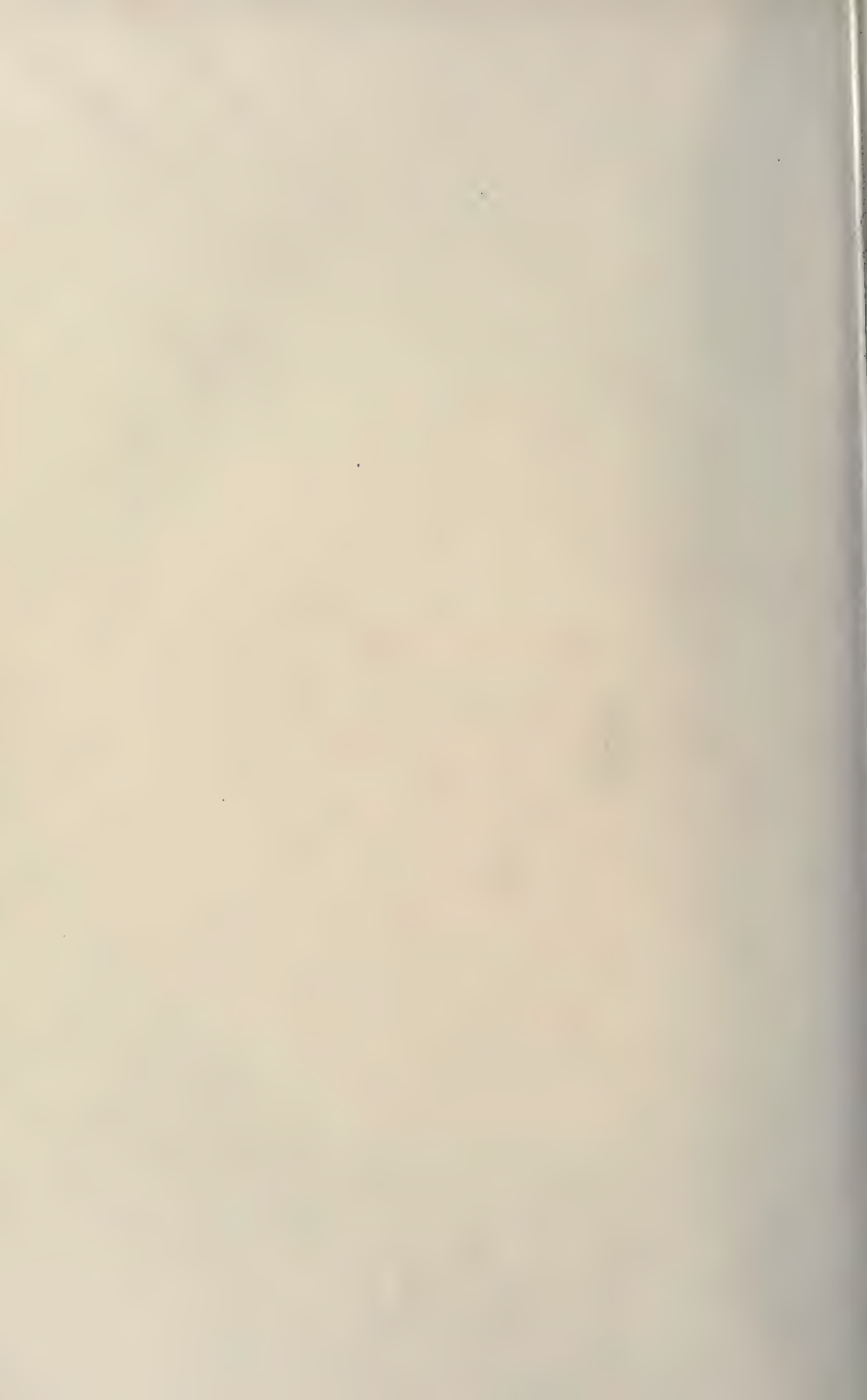
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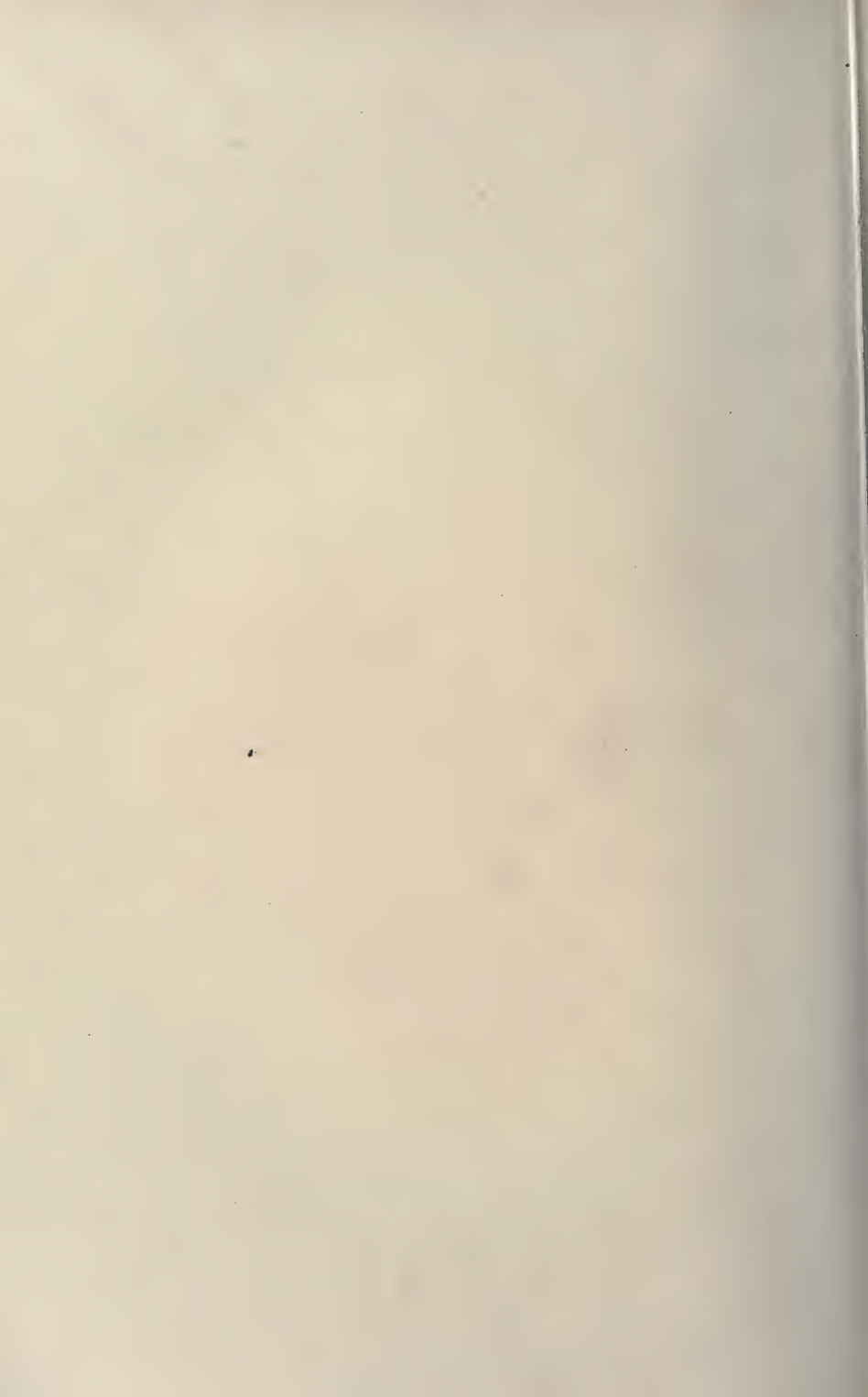
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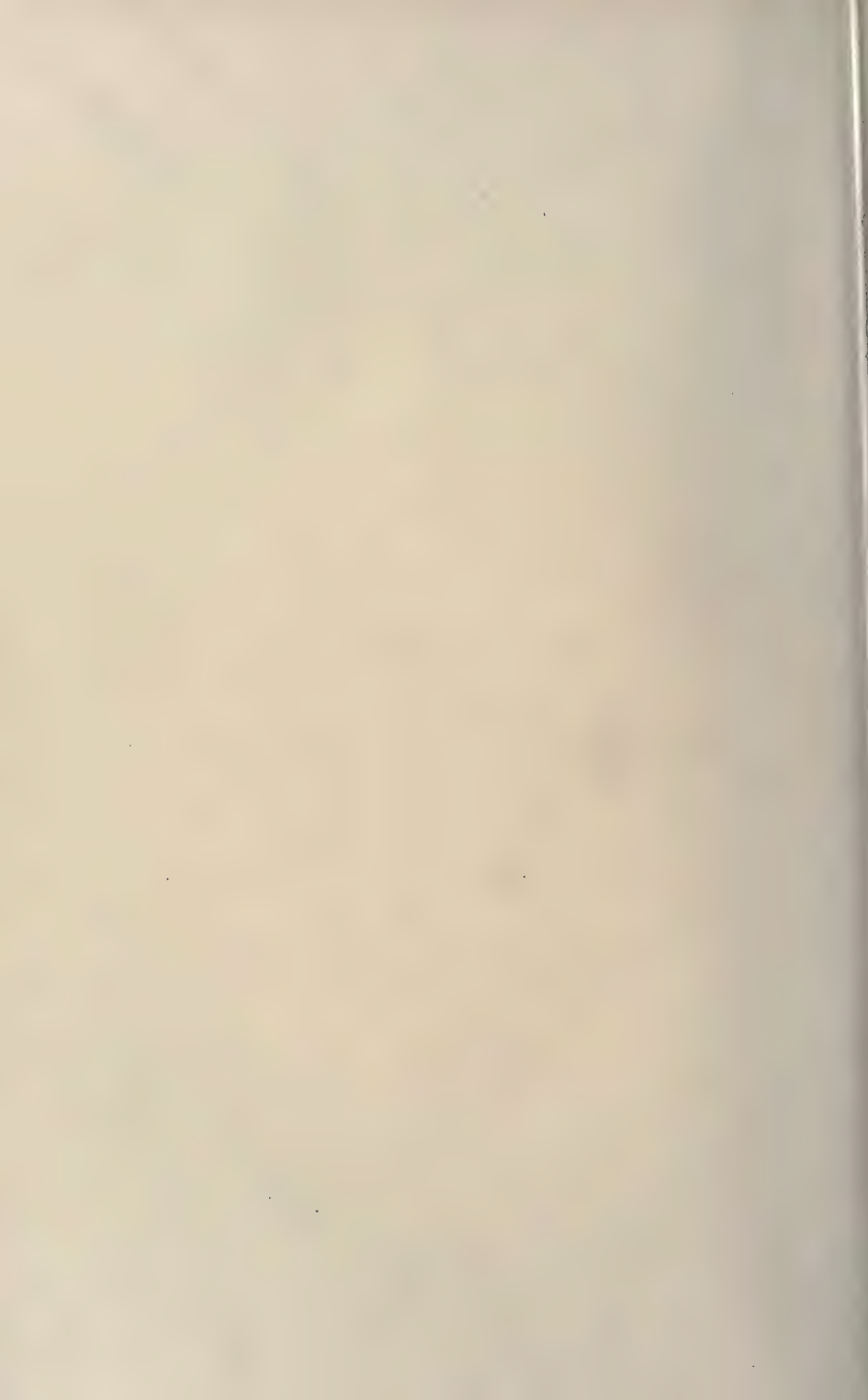
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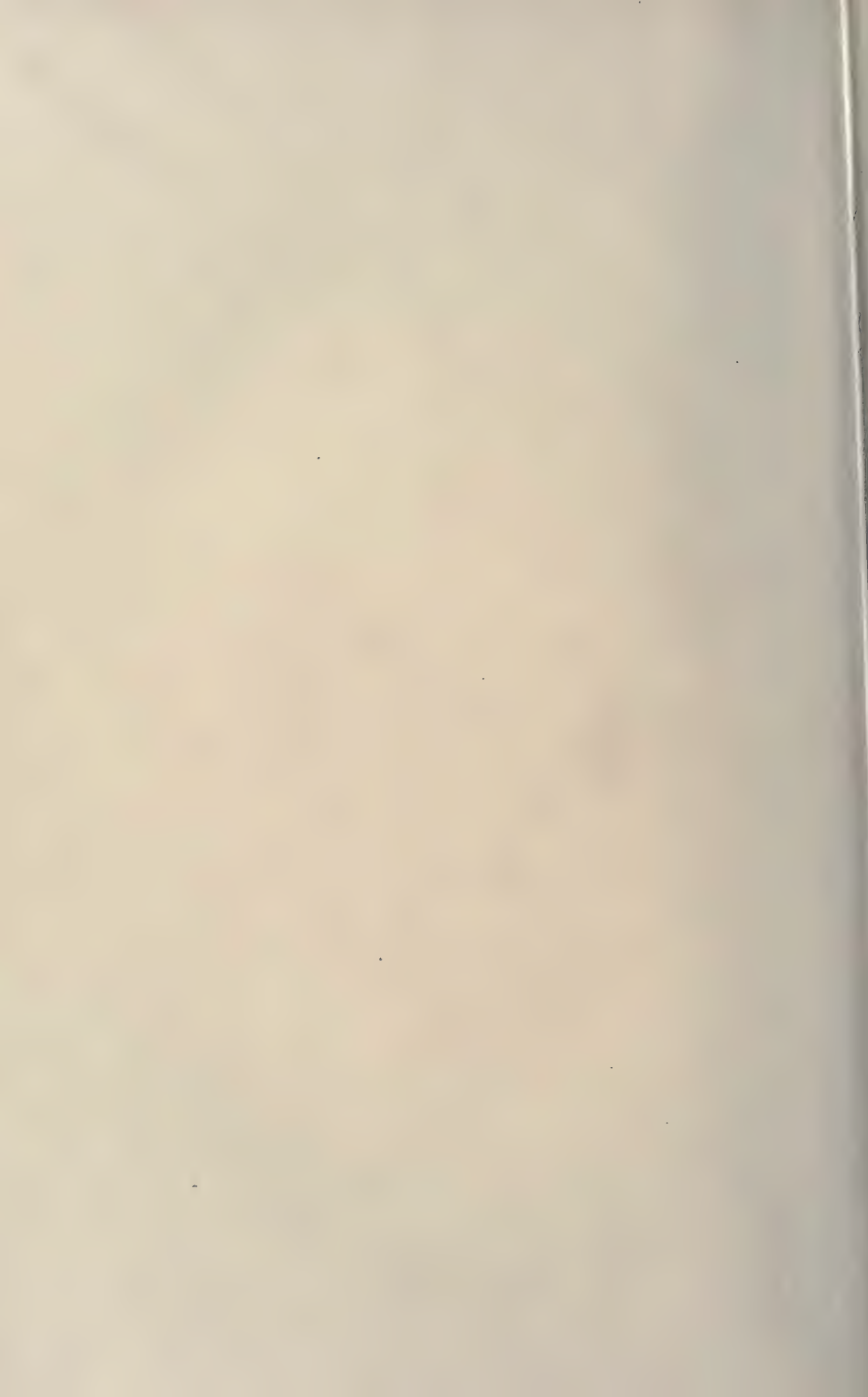
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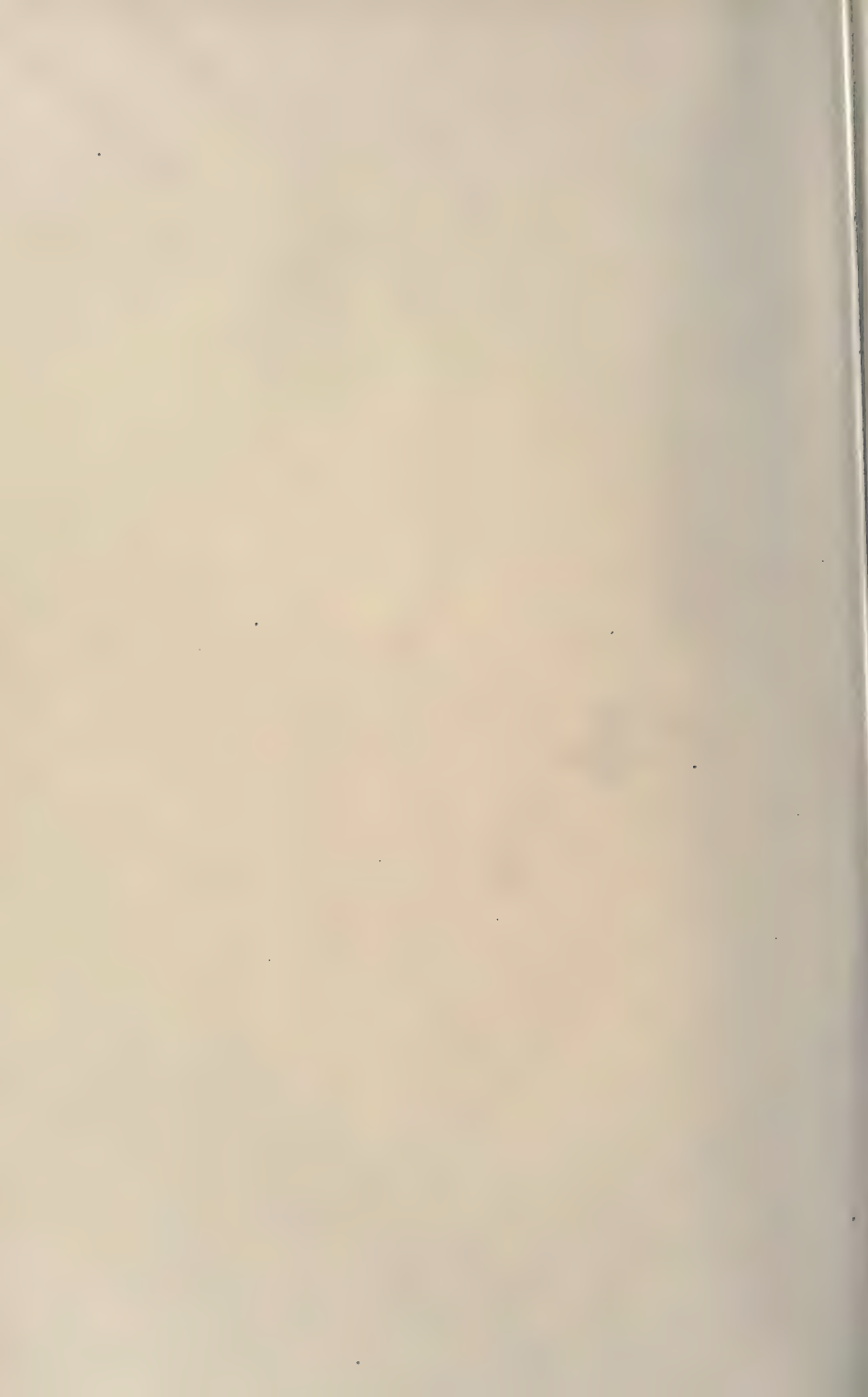
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